

DIMENSIONS OF SPECIMENS

All dimensions given below are in millimetres. D = diameter, Wb = whorl breadth; Wh = whorl height, U = umbilical diameter. Figures in parentheses are ratios expressed as a percentage of the total diameter.

SUTURE TERMINOLOGY

The suture terminology of Wedekind (1916) reviewed by Kullmann & Wiedmann (1970) is followed here. I = internal lobe; U = umbilical lobe; L = lateral lobe; E = external lobe.

SYSTEMATIC PALAEONTOLOGY

Phylum MOLLUSCA Cuvier, 1797

Class CEPHALOPODA Zittel, 1884

Order AMMONOIDEA Zittel, 1884

Suborder ANCYLOCERATINA Wiedmann, 1966

Superfamily ANCYLOCERATAEAE Gill, 1871

Family **Ancyloceratidae** Gill, 1871

Systematics in the family Ancyloceratidae Gill, 1871, are confusing from subfamilial, through generic, and down to specific level. The family Ancyloceratidae is generally taken to consist of the subfamilies Crioceratitinae Wright, 1952, and Ancyloceratinae Gill, 1871 (Wright 1952, 1957; Wiedmann 1962; Thomel 1964; Kakabadze 1981), but may also include the subfamily Helicancylinae Hyatt, 1894 (Casey 1961: 76; Wright 1981: 171; Aguirre Urreta 1986), Protancyloceratinae Breistroffer, 1947 (Wiedmann 1973: 314; Immel 1978: 23), Leptoceratinae Manolov, 1962 (= Leptoceratoidinae Thieuloy, 1966), and Karsteniceratinae Immel, 1987 (p. 118), and tentatively Heteroceratinae Hyatt, 1900 (Immel 1978: 23). Dimitrova took an extreme view (1970: 76) and divided the superfamily Ancylocerataeae into three different families, Himantoceratidae Dimitrova, 1970, Ancyloceratidae Meek, 1876, and Protacrioceratidae Dimitrova, 1970; fortunately this view has found little support.

Our material primarily addresses the relationship between the often strongly ornamented Barremian crioceratitids referred to *Emericiceras* in the Tethyan Realm, *Paracrioceras* in the Boreal Realm, and *Cryptocrioceras* in the South Gondwanid Region (Zululand, Mozambique and southern Patagonia) respectively, and *Crioceratites* s.s., and their relationship to the co-occurring ancyloceratid genus *Acriceras*. This latter relationship has bearing on the validity of dividing the family Ancyloceratidae into the subfamilies Crioceratitinae and Ancyloceratinae.

Subfamily Crioceratitinae Wright, 1952

Genus *Crioceratites* Leveillé, 1837[= *Emericiceras* Sarkar, 1954; *Paracrioceras* Spath, 1924; *Sornayites* Wiedmann, 1962; *Cryptocrioceras* Aguirre Urreta, 1981]*Type species. Crioceratites duvalii* Leveillé (1837: 313, pl. 22 (fig. 1a-b)).*Discussion*

Typical representatives of the genus *Crioceratites* with loose, crioceratitid coiling have not yet been found in Zululand. Instead, closely coiled forms, some of which had been described under the generic name *Cryptocrioceras* in Patagonia by Aguirre Urreta (1981) occur. In this discussion we concentrate mainly on the systematic position and affinity of '*Cryptocrioceras*' within the genus *Crioceratites*.

The genus *Cryptocrioceras* was introduced by Aguirre Urreta (1981: 114) for *Mantelliceras yrigoyeni* Leanza (1970: 249, pl. 42 (figs 1-2), pl. 43 (fig. 1)) (the type species) and *Acanthoceras hoggi* Leanza (1970: 244, pl. 40 (figs 1-3), pl. 41 (fig. 1)), two species erroneously considered by Leanza to be members of the family Acanthoceratidae, and of Cenomanian age. Freely translated, the diagnosis of *Cryptocrioceras* given by Aguirre Urreta (1981: 114) is as follows:

Of medium size, coiling is evolute with a dorsal zone of impression. The whorl section changes from subtrapezoidal to subquadrate. The ornamentation of the inner whorls consists of strong, trituberculate ribs and intercalatories. Both types pass over the flanks on the whole surface. On the outer whorls all the ribs are the same with smooth bullae. The suture line consists of bifid saddles and trifid lobes, asymmetrical; the lateral lobe is very large and well developed.

Examination of the suture line clearly shows that *Mantelliceras yrigoyeni*, of which *Acanthoceras hoggi* is a synonym, is a typical quadrilobate member of the suborder Ancyloceratina. Also, subsequent detailed stratigraphic collecting in Patagonia has shown the age to be Barremian rather than Cenomanian. *Cryptocrioceras yrigoyeni* is a member of the *Hatchericeras patagonense* assemblage Zone, which occurs above the *Favrella wilckensi* assemblage Zone and below the *Colchidites* assemblage Zone (see e.g. Riccardi 1984a, 1984b; 1988: 57, table 15; Riccardi *et al.* 1987: 120; Riccardi & Aguirre Urreta 1989: 448).

Aguirre Urreta (1981: 116) referred *Cryptocrioceras* to the subfamily Crioceratitinae, and considered the genus to have affinities with *Crioceratites* Leveillé and *Paracrioceras* Spath.

Discovery in Zululand of '*Cryptocrioceras*' *yrigoyeni* and of another (new) species that could be referred to '*Cryptocrioceras*', raises doubts whether it really is necessary to separate this group of crioceratitids from *Crioceratites* s.s., and whether the apparently endemic, Southern Hemisphere occurrence of '*Cryptocrioceras*' is not a taxonomic artefact.

Interpretation of the genus *Crioceratites* is beset with many difficulties, the main problem being whether it is possible, and if so how, to reconcile the names applied to Boreal and Tethyan crioceratitid populations. Monographic descriptions from Boreal and Tethyan regions respectively (e.g. Neumayr & Uhlig 1881; Von Koenen 1902; Sarkar 1955; Thomel 1964) create the impression that there are distinct, geographically separated, Boreal and Tethyan crioceratitid populations. This impression is further strengthened by the apparent parallel (?synchronous) phylogenetic development within *Crioceratites* leading to similar, strongly tuberculate on the inner whorls, yet geographically distinct lineages, e.g. *Paracrioceras* in the Boreal, and *Emericeras* in the Tethyan Realm. To this apparent synchronous development of geographically separate but morphologically related forms, *Cryptocrioceras* from the South Gondwanid Region (southern Patagonia, Zululand and southern Mozambique) can now be added.

Crioceratites s.l. shows a wide range of morphological variation over its geographic and stratigraphic distribution during the Hauterivian and Barremian. The genus is most probably interpreted too widely but, as yet, no satisfactory subdivision has been proposed. Several species groups (e.g. Uhlig 1883; Sarasin & Schöndelmayer 1902; Kilian in Roman 1938: 352; Sarkar 1955; Thomel 1964; Thieuloy & Thomel 1964; Immel 1978, 1979b) and genera or subgenera, e.g. *Emericeras* Sarkar, 1954, and *Paracrioceras* Spath, 1924, and phylogenetic lineages (e.g. Wiedmann 1962) have been recognized within *Crioceratites* but, unfortunately, many of these are either poorly defined or open to question. A full discussion of these attempted subdivisions of the genus *Crioceratites* is beyond the scope of the present investigation, and we limit ourselves to the relevant sections that have bearing on the identity of '*Cryptocrioceras*'.

Within the genus *Crioceratites*, the closest allies to '*Cryptocrioceras*', especially the type species *C. yrigoyeni*, are the strongly trituberculate forms that have been placed in *Emericeras* Sarkar, 1954, in the Tethyan Realm and *Paracrioceras* Spath, 1924, in the Boreal Realm, as was initially indicated by Aguirre Urreta (1981: 117).

The status of *Emericeras* and *Paracrioceras* varies according to different authors. According to Sarkar (1954, 1955, 1977: 260) and mainly French authors (e.g. Thomel 1964, 1981), *Emericeras* is retained for the strongly tuberculate Mediterranean (Tethyan) crioceratitids and *Paracrioceras* for the Boreal equivalents (Sarkar 1977: 260). Wright (1957: L208) included *Emericeras* in the synonymy of *Crioceratites* with a question mark, but maintained *Paracrioceras* as a separate genus.

Wiedmann (1962: 112) regarded both *Emericeras* and *Paracrioceras* as junior synonyms of *Crioceratites* and, in addition, included *Pseudothurmannia* as a subgenus in *Crioceratites* s.l., a view followed here. The most significant aspect of Wiedmann's (1962) work was that he recognized a trend towards recoiling (Fig. 1), and the concurrent reduction or simplification of ornamentation on the outer whorls in some of the Crioceratitinae, leading to near-ammonitic end-

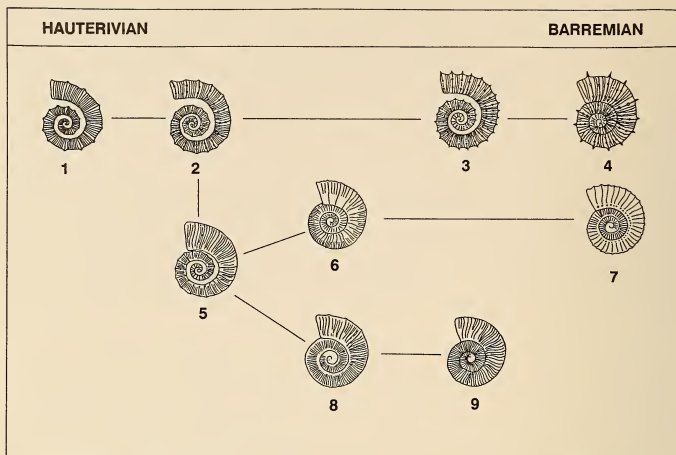


Fig. 1. Suggested phylogeny of major branches of *Crioceratites* to illustrate the trend towards recoiling, according to Wiedmann (1962). 1. *C. (C.) duvali*. 2. *C. (C.) nolani*. 3. *C. (C.) emerici* (= '*Emericiceras*'). 4. *C. (Sornayites) paronai*. 5. *C. (C.) majoricensis*. 6. *C. (Pseudothurmannia) angulicostatus*. 7. *Hemihoplites feraudianus*. 8. *C. (Pseudothurmanni) balearensis* (= '*Balearites*'). 9. *C. (Ps.) balearis ibizensis*. (Redrawn after Wiedmann 1962, text-fig. 35.)

members such as *Pseudothurmannia*, *Hemihoplites* and '*Sornayites*' (Fig. 1), a trend also recognized by Thieuloy (1964) (Fig. 3).

Rawson (1975: 279), commenting on Spath's (1924: 279) reference to the '*emerici*' group in his brief discussion on *Paracrioceras*, regarded *Emericiceras* as a junior subjective synonym of *Paracrioceras* and suggested that the latter might be regarded as a subgenus of *Crioceratites* (see also Rawson & Mutterlose 1983: 138; Rawson 1983: 498).

Immel (1978) followed Wiedmann's (1962) views in regarding both *Paracrioceras* and *Emericiceras* as synonyms of *Crioceratites*. Further, Immel (1978, 1979b), on the basis of the phylogenetic trend towards recoiling, was able to recognize five Mediterranean and three Boreal species groups in *Crioceratites* s.l. (Fig. 2).

Immel's (1978, 1979b) (Fig. 2) grouping of *Crioceratites* is here used merely as a convenient framework for discussing some of the affinities of the Gondwanid crioceratitid '*Cryptocrioceras*'. A full discussion of the merits and demerits of Immel's species grouping is beyond the scope of the present discussion.

In the Mediterranean region, the group of *Crioceratites* (*C.*) *nolani* bears some resemblance to '*Cryptocrioceras*'. It is a long-ranging group, occurring

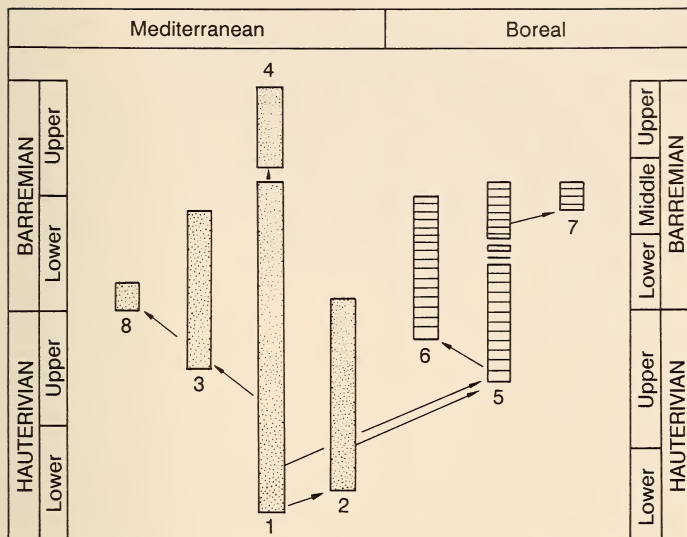


Fig. 2. Arrangement of *Crioceratites* species groups according to Immel (1978, 1979). 1. *C. (C.) nolani*. 2. *C. (C.) quenstedtii*. 3. *C. (C.) majoricensis*. 4. *C. (C.) barremensis*. 5. *C. (C.) hilde-siensi*. 6. *C. (C.) fissicostatus*. 7. *C. (C.) denckmanni*. 8. *C. (Pseudothurmannia) mortileti*. (Redrawn after Immel 1979, text-fig. 3.)

from the Lower Hauterivian to the Upper Barremian, which could make it a potential ancestral group. In the group of *Crioceratites* (*C.*) *nolani*, the species closest to '*Cryptocrioceras*', especially its type species, are *Crioceratites* (*C.*) *emerici* Leveillé (1837: 314, pl. 23 (fig. 1) (see Immel 1978: 35, table 4a) and *C. (C.) thiollierei* (Astier, 1851: 18, pl. 5 (fig. 7) (see Immel 1978: 35, table 4b), both from the Lower Barremian. These are typical '*Emericiceras*'. *Crioceratites* (*C.*) *thiollierei* (including *Emericiceras ottohaasi* Sarkar (1955: 95, pl. 6 (fig. 5) and *Emericiceras thiollierei* Ast. sp. var. *multicostata* Sarkar (1955: 93, pl. 4 (fig. 22), pl. 10 (fig. 6)) is closest to '*Cryptocrioceras*' *yrigoyeni*. The style of ornament, consisting of strong trituberculate ribs, separated by variable intermediaries that themselves may bear tubercles, and the formation of loops between the tubercles, are all features found in '*Cryptocrioceras*' *yrigoyeni*. The modes of coiling, however, are totally different. Coiling in *Crioceratites* (*C.*) *thiollierei* is distinctly crioceratitid, loose, and some specimens uncoil in the adult stage (Thomel 1964: 35, text-fig. 4) and may even form a recurved hook (Immel 1978: 40) (Fig. 4).

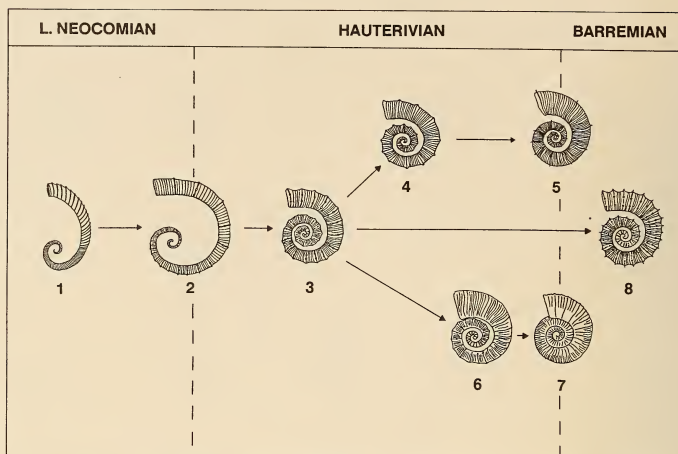


Fig. 3. Suggested phylogeny of major branches of *Crioceratites* to illustrate trend towards recoiling according to Thieuloy (1964). 1. *Protancyloceras kurdistanense*. 2. *Himantoceras trinodosum*. 3. *Crioceratites* (*C.*) *nolani*. 4. *C. (C.) duvali*. 5. *C. (C.) villersianus*. 6. *C. (C.) majoricensis*. 7. *C. (Pseudothurmannia) angulicostata*. 8. *C. (Emericiceras) emerici*. (Redrawn after Thieuloy 1964, text-fig. 3.)

As far as the strong trituberculation of the major ribs and the low number of intermediaries on the inner whorls are concerned, '*Cryptocrioceras*' finds its closest match in the group of *Crioceratites* (*C.*) *barremense* (Kilian, 1895). Species referable to this group include *C. (C.) barremense* (Kilian, 1895: 978; see also Simionescu 1900: 14, pl. 1 (figs 4-5)), *C. (C.) thomeli* Immel, 1978 (= *Crioceratites* (*Emericiceras*) *collignoni* Thomel, 1964: 33, pl. 6 (fig. 4), text-fig. 3), *C. (C.) alpinus* (d'Orbigny, 1850: 100; see also Cottreau 1937: 63, pl. 78 (figs 16-17)), and *C. (C.) janus* Thieuloy, 1979: 310, pl. 2 (figs 1-4)). The Upper Barremian occurrence of this species group also matches that of '*Cryptocrioceras*'. Unfortunately, very little is known of the overall (adult) shell of these species. From the available figures, however, it does seem that at least *C. (C.) alpinus*, *C. (C.) thomeli* and, to a lesser extent, *C. (C.) barremense* have open, crioceratitid coiling, quite unlike that of '*Cryptocrioceras*'. *Crioceratites* (*C.*) *janus* has the closest coiling of the group and shows the distinct change from major trituberculate ribbing on the phragmocone to simple ribbing on the body chamber. All the specimens of *C. (C.) janus* figured by Thieuloy (1979) are small in comparison to the other species in this group, and we are not sure if these are all juveniles or possibly micromorphs.

In the group of *C. (C.) quenstedtii* (Ooster, 1860), *C. (C.) binelli* (Astier, 1851: 14, pl. 2 (fig. 2); see also Sarkar 1955: 57, pl. 2 (figs 4, 6); Thomel 1964:

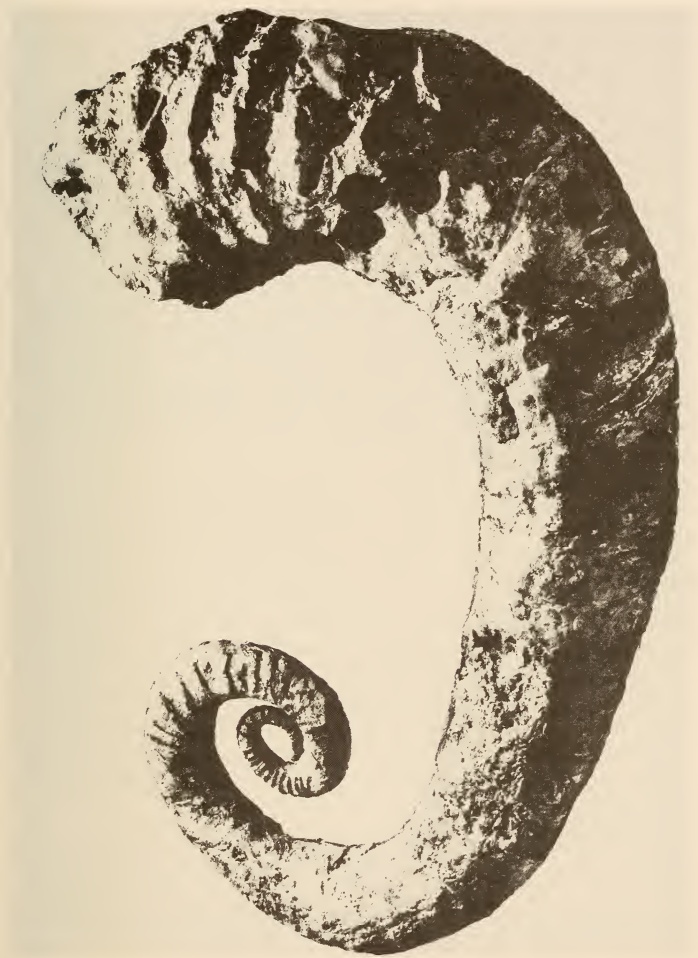


Fig. 4. *Crioceratites (C.) thiollieri* (Astier, 1851). Specimen with fully developed uncoiled stage; collections Staatliches Museum für Naturkunde, Stuttgart, cat. no. 6076, from Escrag-nolles, France. Total length 95 cm. (Photograph supplied by courtesy of Dr G. Dietl.)

28, pl. 3 (figs 2–3)) is similar to *Crioceratites* (*C.*) *australis* sp. nov. in the very short trituberculate stage on the inner whorls. *Crioceratites* (*C.*) *binelli* may also develop constrictions on the outer whorls, as in *Crioceratites* (*C.*) *australis*, albeit associated with major ribs. The ribs on the outer whorls of *C. (C.) binelli* diverge from radially elongated umbilical tubercles. This type of ornament on the outer whorls of *C. (C.) binelli* is unknown in '*Cryptocrioceras*'.

Although similarities in style of ornament can be found between '*Cryptocrioceras*', especially the type species '*C. yrigoyeni*', and some of the above-mentioned Mediterranean species of *Crioceratites*, none of these possesses the combination of close coiling plus the strong trituberculate ornamentation of the early whorls of '*C. yrigoyeni*'.

Close coiling (albeit not with a dorsal zone of impression) associated with strong ornamentation of the inner whorls is known in the Boreal '*Paracrioceras*', especially in the group of *Crioceratites* (*C.*) *denckmanni* (Müller, 1892) (sensu Immel 1978: 63). This species group includes *C. (C.) denckmanni* (Müller, 1892: 18; see Von Koenen 1902: 261, pl. 11 (figs 1–2)) and *C. (C.) stadlaenderi* (Müller, 1892: 19; see Von Koenen 1902: 274, pl. 6 (fig. 6)), both from the Middle Barremian of north-west Germany. *Crioceratites* (*C.*) *denckmanni* is also known from Western Morocco.

Again, none of the above-mentioned Boreal crioceratitids has quite the close coiling and inner trituberculate ornamentation of '*Cryptocrioceras*'.

A similar, though not identical, combination of these features is, however, found in a very poorly known group of crioceratitids for which Wiedmann (1962: 140 footnote) proposed the subgenus *Sornayites* (type species *Emericeras paronai* Sarkar, 1955 = *C. emerici* in Parona 1898: 142, pl. 17 (fig. 6)). According to Wiedmann (1962: 140), *Sornayites* represents another branch within *Crioceratites* in which recoiling had taken place (see also Fig. 1). It differs from the other recoiled groups, however, in that trituberculation persists to the outer whorls. Wiedmann (1962: 140 footnote) thought that '*Sornayites*' originated in the group of *Crioceratites emerici*. Apart from the type species, Wiedmann also included *Crioceratites edouardi* (Honnorat-Bastide, 1889: 462, pl. 11) and *Crioceratites crioceroides* (Torcapel, 1884, pl. 8 (fig. 1)) in *Sornayites*. (Sarkar (1955) and Busnardo (1970) regarded *C. edouardi* and *C. crioceroides* as representatives of *Pseudothurmannia*.)

Thomel (1965: 419) regarded the name *Sornayites* as superfluous and preferred to refer to it as the species group of *C. edouardi*—a view supported by Immel (1978: 11). '*Sornayites*' is poorly known from the Lower Barremian of southern France, northern Italy, Romania, and southern USSR (*vide* Wiedmann 1962: 141 footnote). [Dr G. Delanoy, letter 4.01.1990, informed H.C.K. that '*Sornayites*' *edouardi* may occur as early as Upper Hauterivian—which widens the gap between *Sornayites* and *Cryptocrioceras* even further. He has also found forms resembling *Cryptocrioceras* in a condensed sequence in the Upper Barremian of south-east France.] The combination of close coiling and strong trituberculation of '*Sornayites*' are very similar to those of '*Cryptocrioceras*',

except that in the latter coiling tends to become even closer and there is a reduction of trituberculate ornamentation from the inner whorls outwards. It would seem possible to regard '*Sornayites*' in the Lower Barremian as ancestral to '*Cryptocrioceras*' in the Upper Barremian but it cannot be proven. Even if this suggested phylogenetic sequence is not wholly true, the features of '*Cryptocrioceras*' are by no means so unique as to merit generic separation from *Crioceratites* s.l. The features of '*Cryptocrioceras*' are as far removed from the mainstream of *Crioceratites* as are '*Emericiceras*' or '*Paracrioceras*'.

In the discussion on possible dimorphism (see p. 129), we also note that '*Cryptocrioceras*' occurs with *Acrioceras* in Zululand—a situation similar to that found in Boreal and Tethyan Europe where '*Emericiceras*' and '*Paracrioceras*' also occur associated with *Acrioceras*. Studies on the subfamily Heteroceratinae by Klinger *et al.* (1984), Aguirre Urreta & Klinger (1986), and Klinger (1990) all point to strong palaeobiogeographic affinities between these heteromorph ammonite faunas of the Caucasus, Zululand and Patagonia. With this in mind, there can be no serious palaeobiogeographical objections to referring '*Sornayites*' and '*Cryptocrioceras*' to *Crioceratites* s.s.

Even though it seems possible to connect '*Cryptocrioceras*', via '*Sornayites*', with the genus *Crioceratites*, the morphological similarities and geographic proximity with the predominantly Malagasy crioceratitid genus *Menuthiocrioceras* Collignon, 1949, cannot be disregarded.

This apparently endemic genus was erected by Collignon (1949: 75) (as a subgenus of *Crioceratites*) with type species *Crioceras* (*Menuthiocrioceras*) *lenoblei* Collignon (1949: 76, pl. 11 (4) (fig. 1, 1a)) from the Upper Hauterivian of Belohasifaka (Cercle de Sitampiky), Madagascar. In addition to the type species, *C. (M.) besairiei* Collignon (1949: 77, pl. 10 (3) (fig. 1, 1a, 1b)) and *C. (M.) hourcqi* Collignon (1949: 78, pl. 12 (5) (figs 2, 2a, 3, 3a)), both from the Upper Hauterivian of the same locality, were referred to *Menuthiocrioceras*.

According to Collignon (1949), special features of *Menuthiocrioceras* included the whorl section, which is as wide as high to slightly wider than high, the contiguous whorls with a dorsal zone of impression such as found in *Lytoceras*, trituberculate ornamentation, and lack of an uncoiled section.

Collignon (1949) commented on the similarities between *Menuthiocrioceras* and the Boreal crioceratitids from northern Germany, but also noted similarities to *Pseudocrioceras abichi* (Batsevich & Simonovich, 1873). Finally, Collignon (1949) also noted that the continuity of the ribbing over the venter were features more ancyloceratid than crioceratitid.

In the same paper, Collignon (1949: 79, pl. 12 (5) (fig. 4, 4a)) described *Crioceras* sp.? This specimen has very strongly trituberculate major ribs and we are not sure why Collignon did not refer this specimen to *Menuthiocrioceras* as well. This specimen is, to all appearances, identical to the inner whorls of '*Cryptocrioceras*' *yrigoyeni*.

Later, Collignon (1962) described additional material from the Upper Hauterivian, which he referred to *Menuthiocrioceras*. These include *M. colcanapi*

Collignon (1962: 78, pl. 202 (figs 918–919)), *M. kuntzi* Collignon (1962: 80, pl. 206, figs 920–921)), *M. ampakabense* Collignon (1962: 82, pl. 207 (figs 922–923)), *M. aontzyense* Collignon (1962: 82, pl. 207 (fig. 924)), *M. sornayi* Collignon (1962: 84, pl. 208 (figs 925–926), p. 86, pl. 209 (fig. 927)), *M. sarkari* Collignon (1962: 88, pl. 210 (fig. 928)), and *M. mahafalense* Collignon (1962: 90, pl. 211 (fig. 929)). These specimens show the extreme variability of *Menuthiocrioceras* as interpreted by Collignon. *Menuthiocrioceras* is very large by normal crioceratitid standards—with estimated phragmocone diameters of 30–40 cm (see e.g. *M. sornayi* in Collignon 1962, pl. 208 (fig. 925)), with ornament varying from densely ribbed (e.g. *M. kuntzi*) to very faint as in *M. sarkari*. Flared trituberculate ribs may occur in large fragments of *M. sornayi* (e.g. pl. 209 (fig. 927)); others seem to have only faint trituberculate ribbing. Distinct constrictions occur in *M. ampakabense*.

In addition, Collignon (1962: 20, pl. 431 (fig. 821)) also described *Menuthiocrioceras* sp. indet. from the Lower Valanginian of Antsalova.

The genus *Menuthiocrioceras* is known mainly from Madagascar, but was also recently recorded from Indonesia (Skwarko & Thieuloy 1989). *Crioceratites diamantensis* (Gerth, 1925) (see Gerth 1925: 115, pl. 1 (figs 3–4); Giovine 1950: 53, pl. 5 (fig. 1), pl. 6 (figs 2–3); Riccardi 1988 pl. 7 (figs 1–2)) from the Upper Hauterivian–Lower Barremian of the Neuquén Basin of Patagonia, which also has close coiling, may also belong to *Menuthiocrioceras*.

In view of the variation shown in Malagasy *Menuthiocrioceras*, it is difficult on morphological grounds alone, to find any valid reasons for maintaining '*Cryptocrioceras*' and *Menuthiocrioceras* separate. A problem in this connection is that we do not have any material between the last occurrence of *Menuthiocrioceras* in the Upper Hauterivian, and the first occurrence of '*Cryptocrioceras*' in the upper part of the Lower Barremian or lower Upper Barremian—but this is also the case between '*Sornayites*' and '*Cryptocrioceras*' and thus cannot alone be regarded as a convincing argument.

The main problem in relating *Menuthiocrioceras* to '*Cryptocrioceras*', or to the rest of the crioceratitids for that matter, lies in the close coiling of the former. The very earliest forms of *Menuthiocrioceras* in the Lower Valanginian (see e.g. Collignon 1962: 20, pl. 181 (fig. 821))—this could possibly be an uncoiled neocomitid and not a crioceratitid (Dr P. F. Rawson pers. comm.)), are already closely coiled with a distinct dorsal zone of impression, as also are the better known forms from the Upper Hauterivian. If *Menuthiocrioceras* is to be considered as ancestral to *Crioceratites*—as tentatively suggested by Wiedmann (1973)—or possibly to '*Cryptocrioceras*', an intermediate group of uncoiled forms has to be envisaged near the Hauterivian–Barremian boundary to connect with loosely coiled *Crioceratites* gr. ex. *C. emerici*. As far as we know, however, the general trend in the Crioceratitinae is towards recoiling (cf. Wiedmann 1962; Thieuloy 1964; Figs 1, 3) rather than uncoiling. This would seem to count against the possibility that *Menuthiocrioceras* may be regarded as a direct ancestor of *Crioceratites* gr. ex. *C. emerici* (and subsequent '*Emerici-*

ceras' and '*Paracrioceras*'). This leaves us with the possibility that *Menuthiocrioceras* connects directly with '*Cryptocrioceras*'. This would not involve any drastic uncoiling in the Lower Barremian, neither would it involve dramatic change in ornament. It would, however, suggest that '*Cryptocrioceras*' evolved independently from *Menuthiocrioceras*, but in parallel with *Emericiceras* in the Tethyan Realm and *Paracrioceras* in the Boreal Realm, from *Crioceratites* s.s.—indeed a remarkable case of convergence.

Thus, although *Menuthiocrioceras* is morphologically very similar to '*Cryptocrioceras*', it seems preferable from phylogenetic, palaeobiogeographic and taxonomic points of view to separate them, and to regard *Cryptocrioceras* as a true *Crioceratites* with affinities to the groups of '*Emericiceras*' and '*Paracrioceras*', and possibly '*Sornayites*'. The exact systematic position of *Menuthiocrioceras* within the *Crioceratitinae* remains an enigma and it is accorded separate generic status.

The ornamentation of '*Cryptocrioceras*' resembles that of *Pseudocrioceras* (type species *Scaphites abichi* Batsevich & Simonovich, 1873). *Pseudocrioceras* was introduced by Spath (1924: 78) by merely indicating the type species. The most comprehensive discussions are by Kakabadze (1978, 1981). *Pseudocrioceras* has an uncoiled straight shaft after the planispiral section, which clearly distinguishes it from '*Cryptocrioceras*'.

Relationships between '*Cryptocrioceras*' and *Pedioceras* Gerhardt, 1897 (type species *Pedioceras cundimarcae* Gerhardt, 1897: 172, pl. 4 (fig. 7)), are difficult to formulate because *Pedioceras* is poorly defined. We do not know if the various species and figured specimens referred to *Pedioceras* by different authors (e.g. Gerhardt 1897; Royo y Gómez 1945; Yenne 1949) in fact all belong to the same genus. If *Pedioceras* is interpreted in terms of Gerhardt's (1897: 170–171) diagnosis and the type species *P. cundimarcae* only, it appears that *Pedioceras* lacks differentiation into major and minor ribs on the inner whorls, and is thus easily distinguished from '*Cryptocrioceras*'. The specimen figured by Yenne (1949, pl. 102 (fig. 1)) appears to be a *Crioceratites*.

The genus *Hoplitocrioceras* Giovine, 1950 (type species (by monotypy) *Hoplitocrioceras gentilii* Giovine, 1950, pl. 4 (figs 1–2)), from the Neuquén Basin of Argentina, is a doubtful evolute *crioceratitid*, being based on a single specimen lacking the inner whorls.

Occurrence

Crioceratites has a world-wide distribution through the Hauterivian to the Upper Barremian. It is best documented from the Tethyan and Boreal regions of Europe but is also known from the Caucasus (e.g. Drushchits & Kudryavtseva 1960; Kotetishvili 1970; Kakabadze 1981); in Africa from Morocco (Roch 1930), Egypt? (H. Douvillé 1916), Somalia? (Tavani 1942), Tanzania? (Spath 1930: 135), Madagascar? (Collignon 1949), Mozambique (Förster 1975), and Zululand (herein); southern Patagonia, Argentina (Austral Basin) (Leanza 1970; Aguirre Urreta 1981); Neuquén Basin (Gerth 1925; Weaver 1931; Giovine

1950, 1952; Camacho & Riccardi 1978; Riccardi 1988); Colombia? (Etayo Serna 1968); Cuba (Myczynski 1977); Antarctica (Thomson 1971, 1974, 1980, 1983); Japan (Obata *et al.* 1975; Obata & Ogawa 1976; Obata *et al.* 1976; Obata *et al.* 1982; Obata & Matsukawa 1984); Arctic Canada (Jeletzky 1964: 58); and questionably Indonesia (Skwarko & Thieuloy 1989).

Crioceratites (Crioceratites) yrigoyeni (Leanza, 1970)

Figs 5B, 6–16, ?30E–F, ?31F–J, 32A, 40

Acanthoceras hoggi Leanza, 1970: 244, fig. 40 (1–3).

Mantelliceras yrigoyeni Leanza, 1970: 249, fig. 42 (1–2), fig. 43 (1).

Crioceratites (Emericiceras) cf. *thiollierei* (Astier) Förster, 1975: 150, pl. 2 (fig. 2).

Emericiceras Kennedy & Klinger, 1975: 274.

?*Emericiceras* sp. Blasco, Nullo & Ploszkiewicz, 1980: 46, pl. 2 (fig. 8).

Cryptocrioceras yrigoyeni (Leanza) Aguirre Urreta, 1981: 117, pls 1–4.

Type

Holotype is the original of *Mantelliceras yrigoyeni* Leanza (1970, fig. 42 (1–2), fig. 43 (1)), housed in the collections of the Servicio Geológico Nacional, Argentina, no. 12483, from the lower part of the Río Belgrano Formation, at Chorrillo Rivera, Santa Cruz Province, Argentina.

Material

BMNH C80003–4, C80039, C80055–80089, SAM–PCZ8424a–b, PCZ8425a–b, PCZ8430–8431, PCZ8433–8435, PCZ8437–8438, PCZ8445–8448, PCZ8453, all from locality 170, cliff and gully sections 2 km north-west of Mlambongwenya Trading Store on the north side of the stream, Makatini Formation, Barremian I–II. Some of the specimens are precisely located within this cliff section: SAM–PCZ8447 is from Bed 17; PCZ8446 from Bed 18; PCZ8431 and PCZ8435 from Bed 19; PCZ8437 from Bed 21; PCZ8445 from Bed 23; and PCZ8425a–b and PCZ8453 from Bed 25.

Dimensions

<i>Specimen</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>
C80066	45	12,5 (27,7)	18 (40,0)	0,69	15 (33,3)
C80057	26	8,6 (33,0)	10 (38,5)	0,86	11 (42,3)
C80069	38	—(crushed)	—	—	15 (39,5)
C80060	35	11 (31,4)	13 (37,2)	0,85	16 (45,7)
C80055	26,6	11,5 (43,2)	11,4 (42,9)	1,00	11 (41,4)

Description

Our material of this species is very variable as far as coiling of the inner whorls, nature and strength of ornament throughout, and inflation of the whorl section are concerned. Coiling on the inner whorls is crioceratitid, with major trituberculate and intermediary, tuberculate or non-tuberculate ribs, becoming closer coiled on the outer whorls where the ribs become non-tuberculate and uniform.

Coiling on the inner whorls is very variable, ranging from open crioceratitid with the whorls not touching at all, as in PCZ8447 (Fig. 30E), through slightly less open with only the third whorl being detached from the preceding one, as in PCZ8425b (Figs 16, 31F-I), to close crioceratitid, as in PCZ8433 (Fig. 31J), PCZ8424a-b (Fig. 32A), C80056, and C80055 (Fig. 6A-B). The ventral spines of one whorl generally touch a shallow impressed zone of the preceding whorl, but the main surface of the dorsum and venter do not seem to have been in contact. This appears also to be the case in later whorls, the dorsum of which is also impressed, and which also shows what appear to be depressions to house spines (e.g. Fig. 10D).

The whorl section varies from compressed to depressed, with the greatest breadth at the umbilical spine. In general, ornament is strongest in inflated individuals and weakest in compressed ones; it will be convenient to describe the species in these terms.

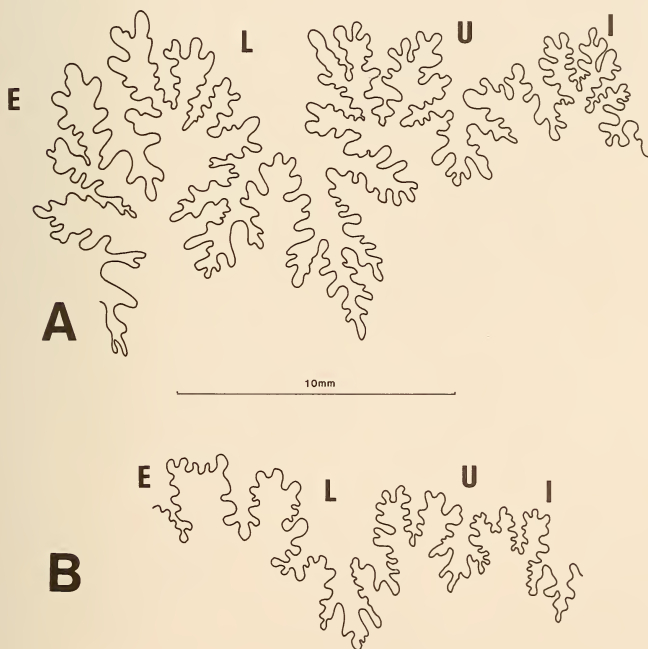


Fig. 5. A. *Crioceratites* (*C.*) *australis* sp. nov., BMNH C80054. B. *Crioceratites* (*C.*) *yrigoyeni* (Leanza, 1970), BMNH C80057. Suture lines.



Fig. 6. *Crioceratites* (*C.*) *yrigoyeni* (Leanza, 1970). A-B. BMNH C80055. $\times 1.5$.

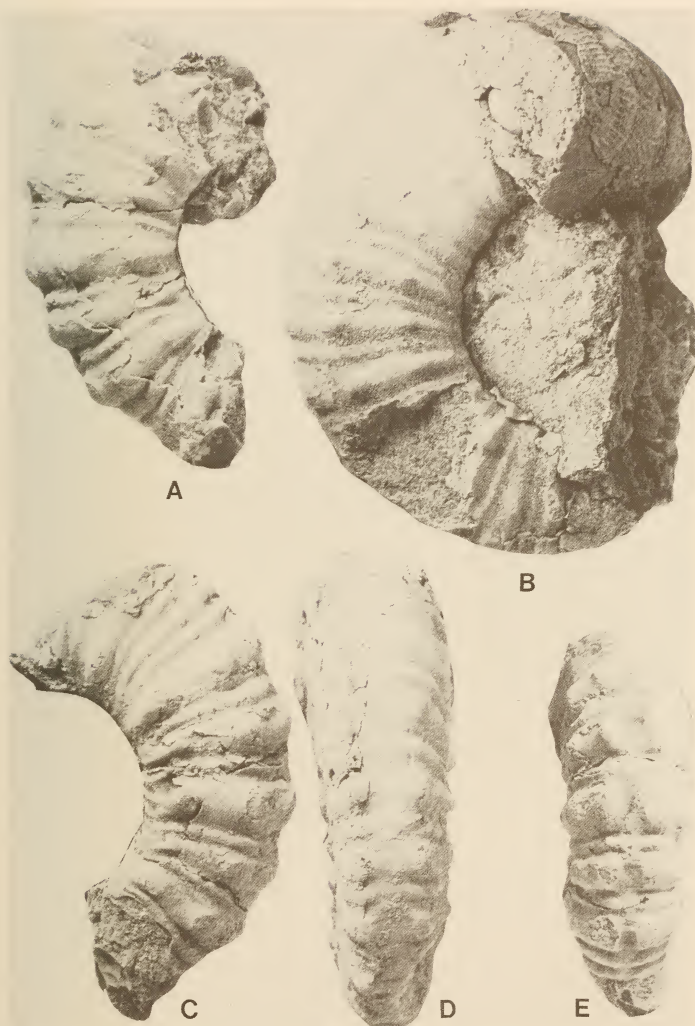


Fig. 7. *Crioceratites* (*C.*) *yrigoyeni* (Leanza, 1970). A, C, E. BMNH C80075.
B, D. BMNH C80066. All $\times 2$.

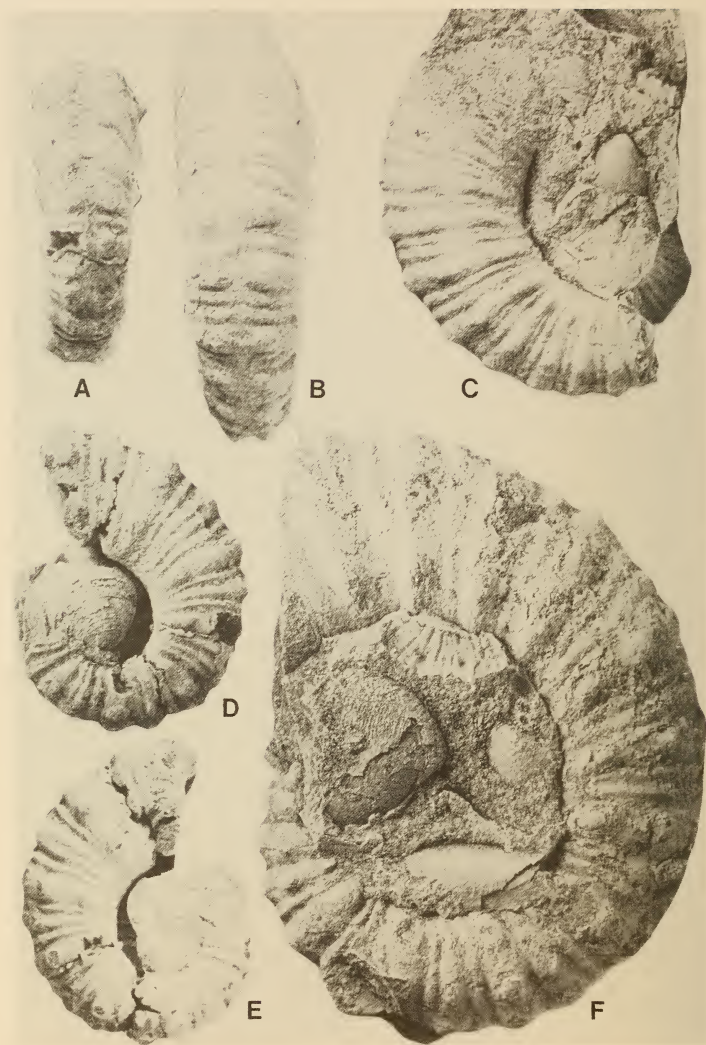


Fig. 8. *Crioceratites (C.) yrigoyeni* (Leanza, 1970). A, D-E. BMNH C80057.
B-C. BMNH C80073. F. BMNH C80004. All $\times 2$.



Fig. 9. *Crioceerates* (*C.*) *yrigoyeni* (Leanza, 1970). A-C. BMNH C80004. All $\times 2$.

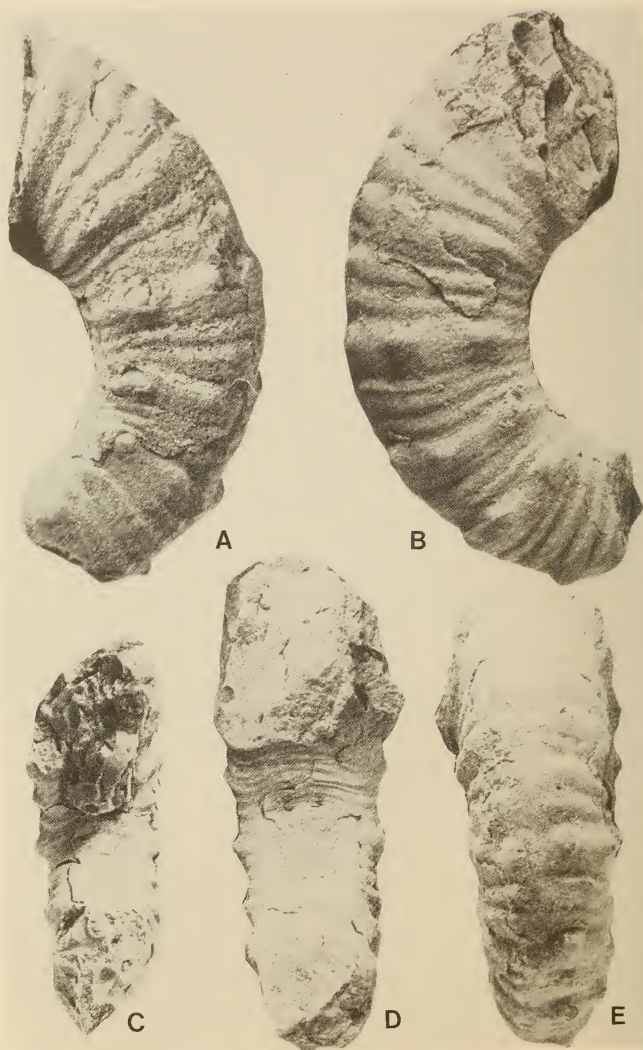


Fig. 10. *Crioceratites* (*C.*) *yrigoyeni* (Leanza, 1970). A-B. BMNH C80058.
C-E. BMNH C80075. All $\times 2$.

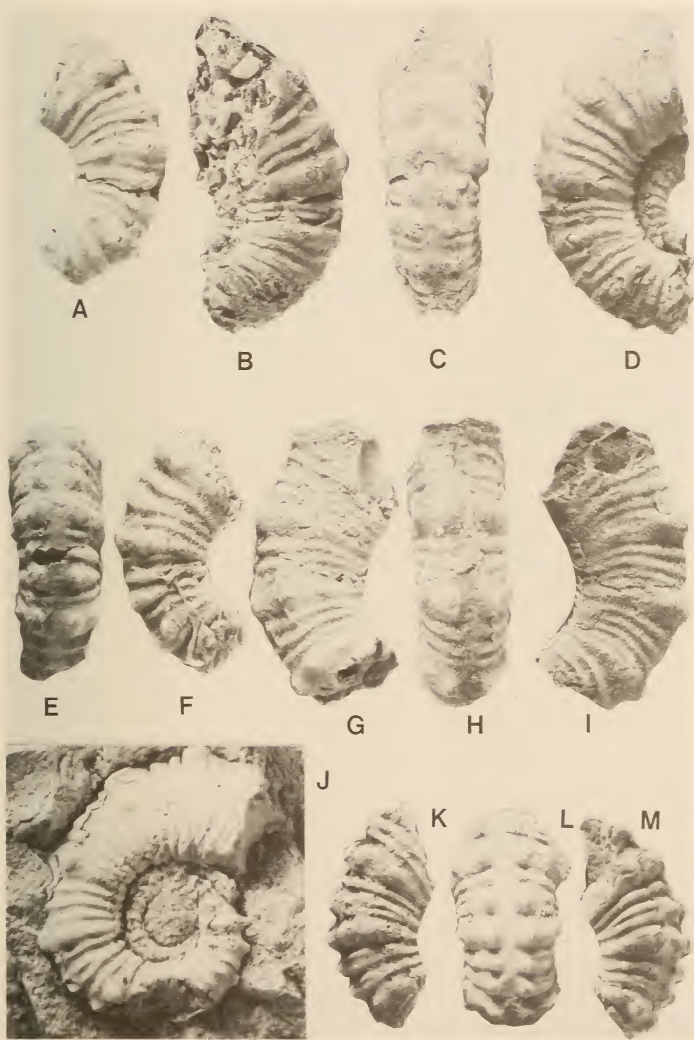


Fig. 11. *Crioceratites (C.) yrigoyeni* (Leanza, 1970). A, E-F. BMNH C80081. B-D. BMNH C80078. G-I. BMNH C80080. J. BMNH C80059. K-M. BMNH C80079. A, E-F, J $\times 3$; B-D, H-I $\times 1$.

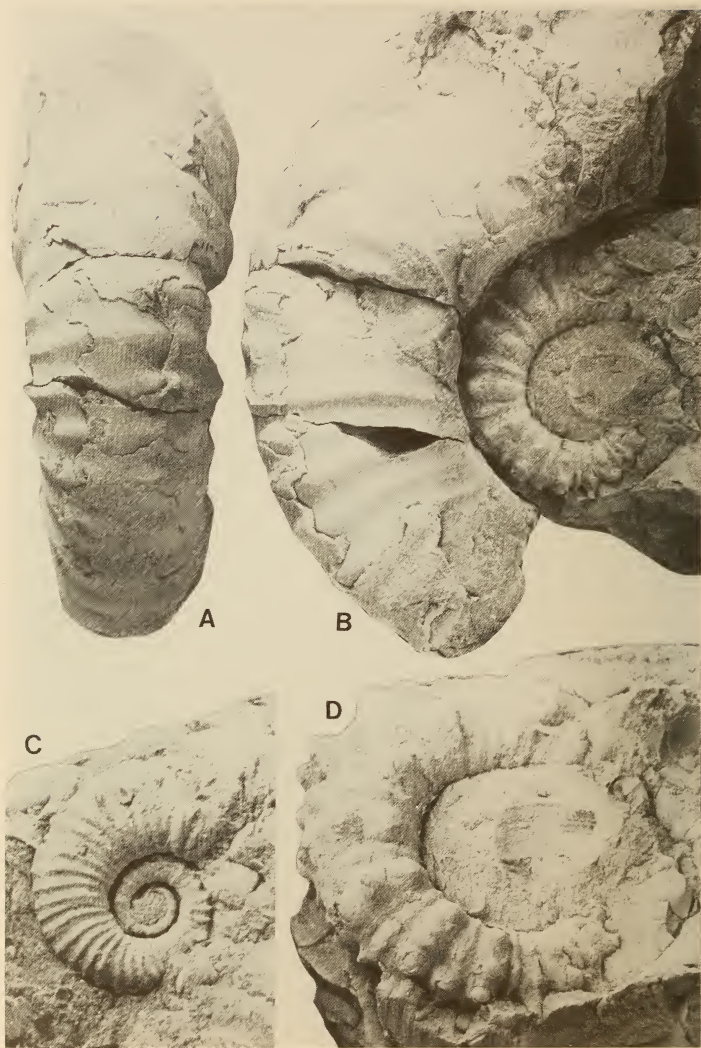


Fig. 12. A-B. *Crioceratites* (C.) *yrigoyeni* (Leanza, 1970). BMNH C80003. C. *Acrioceras* (A.) *zulu* sp. nov. BMNH C80007. D. *Crioceratites* (C.) *yrigoyeni* (Leanza, 1970). BMNH C80060.
A-B $\times 1$; C $\times 4$; D $\times 2$.

Inflated forms: The innermost whorls are smooth and with rounded whorl section but, at a diameter of c. 4–5 mm, the whorl section is distinctly coronate, depressed as seen in C80055 (Fig. 14) and PCZ8425b (Fig. 16). There are about 20–25 ribs per whorl. These arise on the umbilical wall and bear faint conical to radially elongate tubercles on the inner edge of the umbilical wall. Very strong, rounded tubercles occur at or slightly below midflank. When well preserved, these are revealed as the bases of short, wedge-shaped spines; from them, the ribs pass straight across the flanks and bear prominent ventrolateral tubercles that are the bases of sharp spines. Already at this diameter, the lower two rows of tubercles are more prominent on some ribs than on others.

With increase in size, the umbilical tubercles migrate to a lower-lateral position, and the other two rows to an inner and outer ventrolateral position, respectively. Differentiation in strength of ribbing becomes more prominent with the addition of secondary ribs that are very variable both in form and number, as shown by Figures 6–13.

At one extreme is a single, relatively weak rib bearing no, or only small, ventrolateral spines. Others may bear umbilical/lateral and upper ventrolateral tubercles or lower and upper ventrolateral tubercles only, with up to four minor ribs between the major in some individuals. Furthermore, the numbers of secondary ribs may be either variable or constant in different individuals and has no apparent taxonomic significance. Attendant on this proliferation of ribs is a change in their direction from prorsiradiate to radial in some specimens, and from straight to convex in all. Between tubercles, ribs are generally single but, in some specimens where preservation is good, distinct looping is visible, and up to four ribs may connect between the tubercles on the flanks. In some individuals (e.g. Fig. 12D), very long, hollow septate spines survive, whereas in others the ribs efface over the siphonal region.

At a diameter of c. 45 mm, tuberculation begins to decline markedly in C80055 (Fig. 6) and there follows a stage of dense, relatively even, flexuous ribbing with single, long ribs and some intercalated ribs, occasional weak, radially elongated bullae low on the flank, no obvious tubercles (but a thickened rib) at the ventrolateral shoulder, and ribs that broaden and weaken across the siphonal area. Some specimens, e.g. C80060, remain strongly tuberculate to greater diameters.

Compressed forms: We have juveniles only of this type, e.g. PCZ8433 (Fig. 31J), C80007 (Fig. 30F), and C80073 (Fig. 8B–C), and they show the same basic pattern of ornament as already described, differing in a higher rib density, generally weaker ribs, elongate bullae rather than conical umbilical/lateral tubercles, weaker lower ventrolateral tubercles that are radially elongate, although retaining strong ventral tubercles on the major ribs. Minor ribs tend to bear only ventral tubercles or none, and ribbing is commonly very subdivided at the ventral midline. In a few specimens the ribbing is particularly flexuous and may be rursiradiate. Occasional pairs of ribs loop to the larger ventral spines.

The suture line of juvenile specimens is shown in Figures 5B and 15. The external lobe (E) is relatively small, the lateral lobe (L) large and asymmetrically trifid, the umbilical (U) small and trifid. The saddle E/L is large and bifid, and L/U and U/I smaller but also bifid.

Discussion

None of our specimens is as large as the Patagonian specimens figured by Aguirre Urreta (1981), but the similar inner whorls leave no doubt that they all belong to the same species. Our material is significant in that it shows the extreme variation, not only in strength of ornament on the inner whorls, but also the differing ratios of major and minor ribs during the course of ontogeny within the same, and also between different specimens. None of our specimens show the adult, body-chamber modifications seen in the Argentinian material with the development of bullae on the ribs and even partial uncoiling in some (e.g. Aguirre Urreta 1981, pl. 4 (fig. b)).

Crioceratites (*C.*) *australis* sp. nov. described below (see p. 98), differs from *C. (C.) yrigoyeni* in having a tuberculate stage of much shorter duration, and the ornament is never as coarse as in the latter. Also, *C. (C.) australis* develops distinct constrictions on the outer whorls; these have never been observed in *C. (C.) yrigoyeni*.

The specimen described and figured by Collignon (1949: 79, pl. 12 (5) (fig. 4, 4a)) from the Upper Hauterivian of Belohasifaka as *Crioceras* sp.?, is indistinguishable from our material. As discussed above (p. 81), the affinities of this specimen are obscure. It may be a fragment of *Menuthiocrioceras*.

Crioceratites (*C.*) *yrigoyeni* has ornament on the inner whorls similar to that of some Mediterranean 'Emericeras' species of some authors (especially Sarkar 1954, 1955; Thomel 1964, 1981). Thomel (1964: 30) recognized six species groups in 'Emericeras'; of these, 'E.' gr. ex. *barremense* (Kilian, 1895) and 'E.' gr. ex. *thiollierei* (Astier, 1851) are closest to *C. (C.) yrigoyeni*. Both are Upper Barremian. Our inflated forms of *C. (C.) yrigoyeni* with strong ornamentation and few intermediary ribs are closest to 'E.' gr. ex. *barremense*, whereas the compressed forms with more intermediate ribs are closest to 'E.' gr. ex. *thiollierei*.

Immel (1978: 52) included the following species in the group of *Crioceratites barremense*: *C. (C.) barremense* (Kilian, 1895), *C. (C.) thomeli* Immel, 1978 (= *Crioceratites* (*Emericeras*) *collignoni* Thomel, 1964: 33, pl. 6 (fig. 4), text-fig. 3), and *C. alpinus* (d'Orbigny, 1850) (see Cottreau 1937: 63, pl. 78 (figs 16-17)). In all three species the trituberculate ribs are dominant over the intermediaries, if present. However, as far as can be seen from the illustrations, they all appear to have open crioceratitid coiling. One specimen figured by Kakabadze (1981, pl. 15) as *Paracrioceras barremense*, however, has close coiling as in *C. (C.) yrigoyeni*, and is difficult to separate satisfactorily on the basis of the figured material, as is the specimen figured by Kakabadze (1981, pl. 3 (fig. 4)) as *Paracrioceras dolloi* (Sarkar).

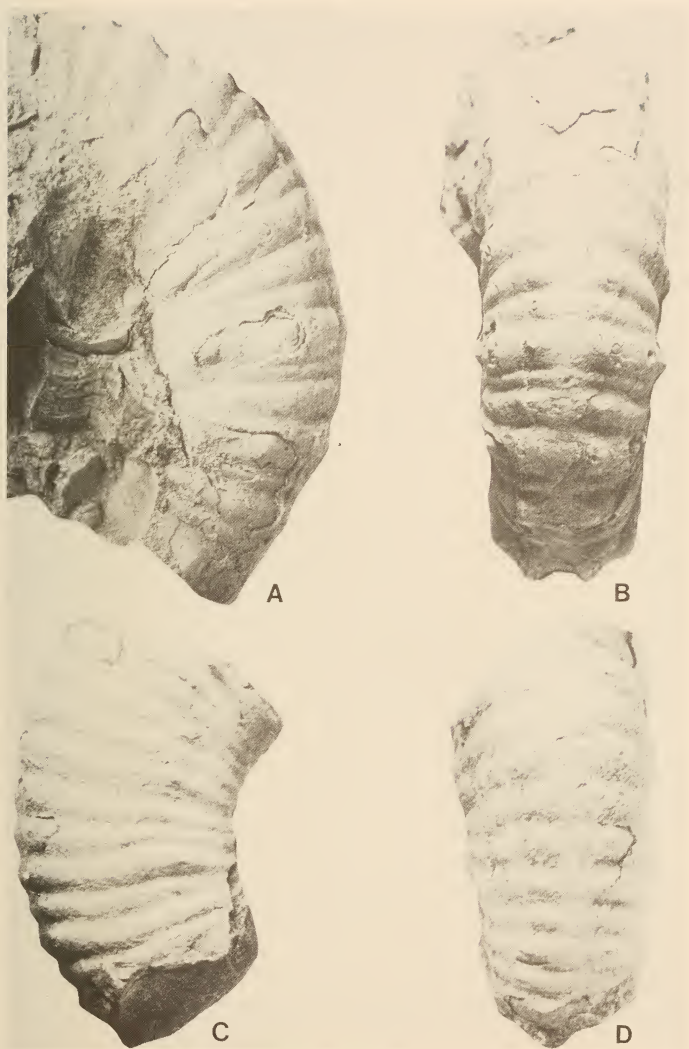


Fig. 13. *Crioceratites* (C.) *yrigoyeni* (Leanza, 1970). A-B. BMNH C80065; $\times 1$.
C-D. BMNH C80039; $\times 2$.

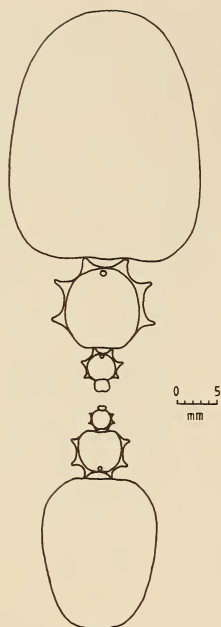


Fig. 14. *Crioceratites (C.) yrigoyeni* (Leanza, 1970). Reconstruction of whorl section of BMNH C80055. $\times 2,1$.

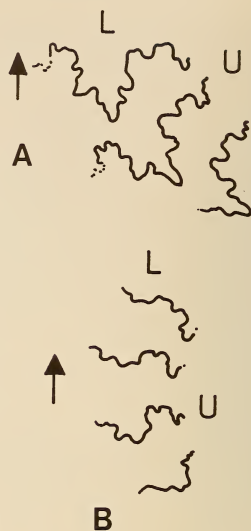


Fig. 15. *Crioceratites (C.) yrigoyeni* (Leanza, 1970). Suture lines. A. SAM-PCZ8433. B. BMNH C80055. A $\times 8,2$; B $\times 11,7$.



Fig. 16. *Crioceratites (C.) yrigoyeni* (Leanza, 1970). Whorl section of SAM-PCZ8425b.

Aguirre Urreta (1981: 119) also compared *C. (C.) yrigoyeni* with *Crioceratites hoheneggeri* (Uhlig, 1883) (in Thomel 1964: 32, pl. 6 (figs 2–3)), but the coiling in this species is also more open crioceratitid than in *C. (C.) yrigoyeni*.

Crioceratites janus Thieuloy (1979: 310, pl. 2 (figs 1–4)), from the Upper Barremian of the Southern Vercors Mountains and referred to the group of *C. barremense* by Thieuloy, is very similar to *C. (C.) yrigoyeni*. It has strong trituberculate ribs on the inner whorls, separated by single intermediaries, but this mode of ornament soon gives way to slightly flexuous, sometimes bifurcating ribbing. Coiling in *C. janus* is also relatively tight and comparable to that of *C. (C.) yrigoyeni*, and not at all as loosely coiled as in typical *C. barremense*, *C. thomeli* or *C. alpinus*. Unfortunately, all available figured specimens of *C. janus* are small, and we do not know if they are juveniles or small adults.

Crioceratites (C.) thiollierei (Astier, 1851: 18, pl. 5 (fig. 7)) resembles our compressed forms as far as the ornament is concerned, but has distinct crioceratitid coiling (see e.g. Thomel 1981: 49, fig. 85). According to Thomel (1964: 30) the species in the group of *C. thiollierei* grow to very large size—up to 1 m in diameter, and may uncoil (Thomel 1964: 35, text-fig. 4) and even form a recurved hook, as shown in a large specimen housed in the collections of the Staatliches Museum für Naturkunde, Stuttgart (Fig. 4).

The ornamentation on the phragmocone of *Pseudocrioceras*, best known from the Caucasus (see e.g. Rouchadze 1933, 1938; Kakabadze 1978, 1981) is very similar to that of *C. (C.) yrigoyeni* but, as pointed out above and by Kakabadze (1978, 1981), the genus has distinct ancylloceratid uncoiling.

Unfortunately, the material from Alexander Island, Antarctica, initially described and figured by Thomson (1974: 12, pl. 2e, text-fig. 4a) as *Emericiceras* (?) sp., and subsequently as *Paracrioceras* (Thomson 1983: 410, text-fig. 2), is too poorly preserved for definite identification, but it does superficially resemble *C. (C.) yrigoyeni*.

The early whorls of *C. (C.) yrigoyeni* are indistinguishable from those of coarsely ornamented forms of *Acrioceras zulu* sp. nov. described below (see p. 110). In fact, small, criocone inner whorls could be referred to either genus (see e.g. Figs 30–31). What is more, they occur together. This association and its implications are discussed below.

The specimen described and figured from the Neuquén Basin of Patagonia as *Paracrioceras* cf. *P. emerici* Lev. by Giovine (1950: 59, pl. 5 (fig. 5)) is too poorly preserved for definite identification.

Occurrence

Lower–Middle Barremian of Patagonia, *Hatchericeras patagonense* assemblage Zone. In Zululand, *C. (C.) yrigoyeni* occurs below the zone of abundant *Colchidites vulanensis australis* Klinger et al., 1984, Barremian I.

Crioceratites (Crioceratites) australis sp. nov.

Figs 5A, 17-24

Type

Holotype is BMNH C80037 from Bed 2 at locality 170, cliff and gully sections, 2 km north-west of Mlambongwenya Trading Store, on the north side of the stream, Makatini Formation, Barremian I.

Material

Eighteen specimens, BMNH C80035, 80038, 80040-80054, and SAM-PCZ8452, all from the same locality as the holotype. SAM-PCZ8452 is from the basal bed, Bed 1, of the cliff section.

Description

Loosely coiled but with the later whorls at least in contact, the dorsal impressed zone being distinct, if shallow. The whorl section is typically compressed, trapezoidal, with a broad dorsum, broadly rounded umbilical shoulders, flattened convergent flanks, rather narrowly rounded ventrolateral shoulders, and flattened venter. The greatest breadth is close to the umbilical shoulder.

At the smallest diameter visible (30 mm), ornament consists of distant umbilical bullae giving rise to groups of two to three ribs with three or four single, non-bullate ribs between. All ribs are delicate, narrow, rursiradiate and rather crowded. They flex backwards and are feebly convex to straight on the flanks, broadening towards the ventrolateral shoulder. The ribs, which arise from bullae, are commonly reunited at a conical, lower ventrolateral and clavate upper ventrolateral tubercle; other ribs bear rounded tubercles on the ventrolateral edge, and all ribs are interrupted on the venter at a smooth, siphonal band.

Only one specimen, the holotype C80037 (Figs 17, 18A-C), shows the tuberculate early stage described above. In other specimens, only the second growth stage is visible; here the whorl section is more compressed (whorl breadth to height ratio is 0.7). There are six to nine ribs in a distance equal to the whorl height. These arise at the umbilical shoulder as the feeblest of bullae. They are recti- to feebly rursiradiate, and broaden markedly from the umbilicus towards the ventrolateral shoulder. Varying from straight to flexuous, they terminate in transversely elongated feeble tubercles on either side of a smooth siphonal area up to a whorl height of 15-17 mm, and are mostly long and simple. There is, however, a range of individuals of uniform to variable rib strength and direction. Variation is also pronounced in the shape of the ventral tubercles (they are sometimes conical), and in the prominence and distinctness of the smooth siphonal area. Both tubercles and smooth zone become less prominent as size increases, disappearing at different diameters from individual to individual, and generally associated with a rounding of the venter (Fig. 19A-C).

In our large specimens, ribs may branch conspicuously (Fig. 23) and generally decline in prominence as size increases. Associated with this decline is the appearance of broad, deep, flexuous, prorsiradiate constrictions, bounded in front and behind by parallel ribs, which give even fragments an immediately recognizable and characteristic appearance (Figs 17, 20B, 21E, 22A, 23A, 24B).

The suture is intricately subdivided, with a large, deeply incised external lobe (E) in which there is a large median element. The lateral lobe (L) is large and asymmetrically trifold; the umbilical lobe (U) is smaller but also asymmetrically trifold; and the internal lobe (I) is intricately subdivided. The saddle E/L is



Fig. 17. *Crioceratites* (*C.*) *australis* sp. nov. Holotype, BMNH C80037. $\times 1$.

large and asymmetrically bifid with deep incisions; L/U is smaller but also asymmetrically bifid (Fig. 5A).

Discussion

The (ontogenetically) short trituberculate stage and the appearance of prominent constrictions on the outer whorls is characteristic of this species, and easily separates it from *Crioceratites* (*C.*) *yrigoyeni*, as well as from the majority of other *Crioceratites* species.

Amongst the Mediterranean species, *C. (C.) binelli* (Astier, 1851) (see e.g. Sarkar 1955: 57, pl. 2 (figs 4, 6); Thomel 1964: 28, pl. 3 (figs 2–3); Immel 1978: 43, table 6a) bears some resemblance to *C. (C.) australis* in the relatively tight coiling, short duration of the trituberculate stage on the inner whorls, and in the presence of occasional constrictions. In *C. (C.) binelli*, however, the constrictions are associated with thickened ribs that may bear umbilical and ventral tubercles.

Amongst the Boreal species, *C. (C.) australis* can be compared with *C. (C.) fissicostatus* (Roemer, 1841) (see e.g. Von Koenen 1902: 233, pl. 12 (fig. 2), pl. 22 (figs 1–2)) and especially *C. (C.) fissicostatus* Roemer var. *minor* von Koenen (1902: 236, pl. 23 (figs 1–2)) (= ?*C. (C.) aequicostatus* (von Koenen, 1902) *vide* Immel 1978: 63)) as far as the fine ornamentation on the inner whorls is concerned. As far as can be seen, however, the Boreal species show distinct uncoiling on the outer whorls.

Crioceratites diamantensis Gerth, 1925 (p. 115, pl. 1 (figs 3–4); Giovine 1950: 53, pl. 5 (fig. 1), pl. 6 (figs 2–3); Riccardi 1988, pl. 7 (figs 1–2)), from the Upper Hauterivian–Lower Barremian of the Neuquén Basin of Patagonia, bears some resemblance to *Crioceratites (C.) australis* in the close coiling and presence of constrictions on the outer whorls. An inner, trituberculate stage has not yet been found in *C. diamantensis* and we are not quite sure of its taxonomic position. We suspect that it may be closer to *Menuthiocrioceras* than to *Crioceratites* s.s.

Occurrence

As yet, *C. (C.) australis* is only known from the first division of the Barremian of Zululand.

Subfamily Ancyloceratinae Gill, 1871

Genus *Acrioceras* Hyatt, 1900

[= *Aspinoceras* Anderson, 1938; *Mesocrioceras* Breistroffer, 1952;

Protacrioceras Sarkar, 1955; *Paraspinoceras* Breistroffer, 1952;

Subaspinoceras Thomel *et al.*, 1987]

Type species. *Ancyloceras tabarelli* Astier (1851: 19, pl. 7 (fig. 9)), by original designation of Hyatt (1900: 588).

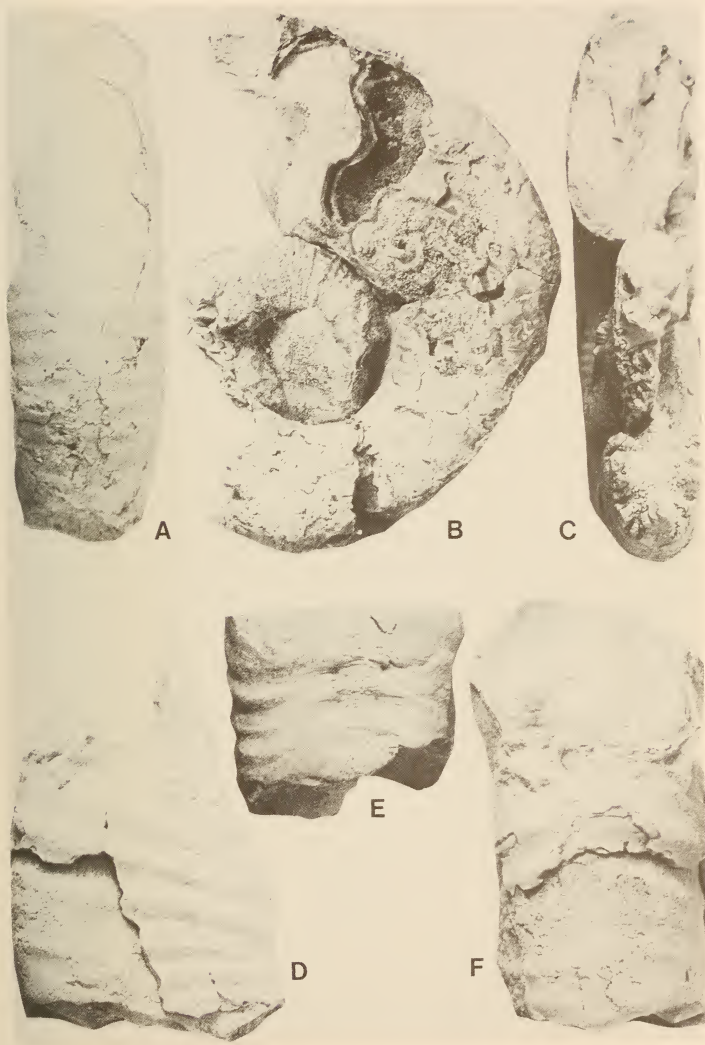


Fig. 18. *Crioceratites (C.) australis* sp. nov. A-C. BMNH C80037, the holotype.
D-F. BMNH C80041. All $\times 1$.



Fig. 19. *Crioceratites* (*C.*) *australis* sp. nov. A-B. BMNH C80052. C-D. BMNH C80038. E. BMNH C80035. All $\times 1$.

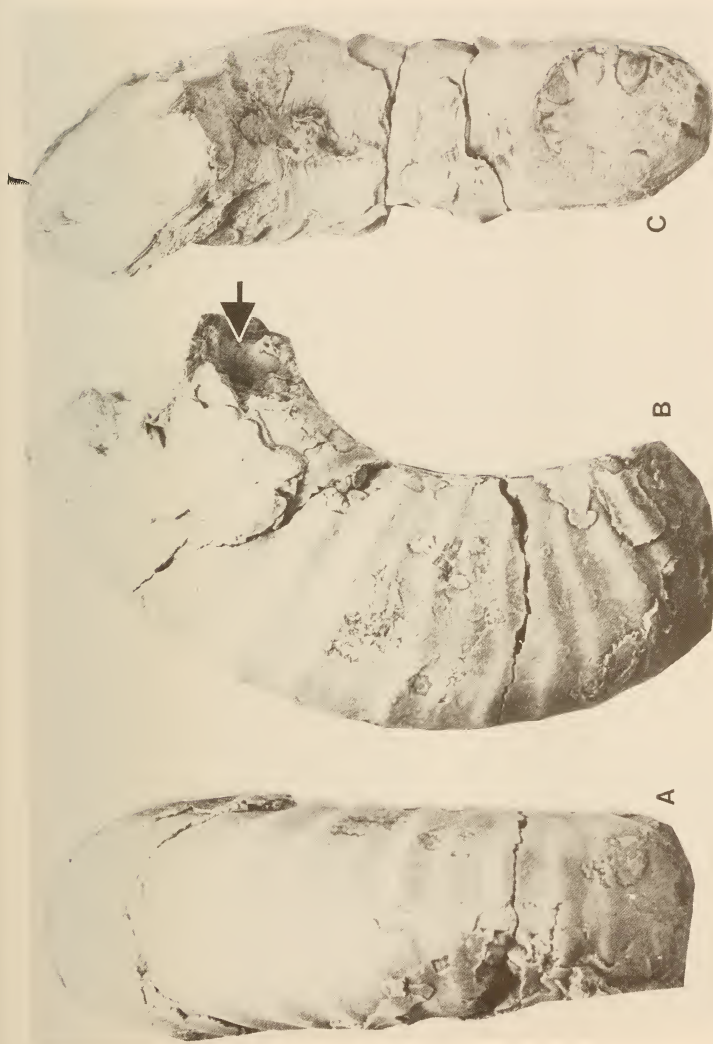


Fig. 20. *Crioceratites* (C.) *australis* sp. nov. A-C. BMNH C80064. Arrow indicates position of fragment of finely ribbed *Acriceras* (A.) *zulu*. All $\times 1$.

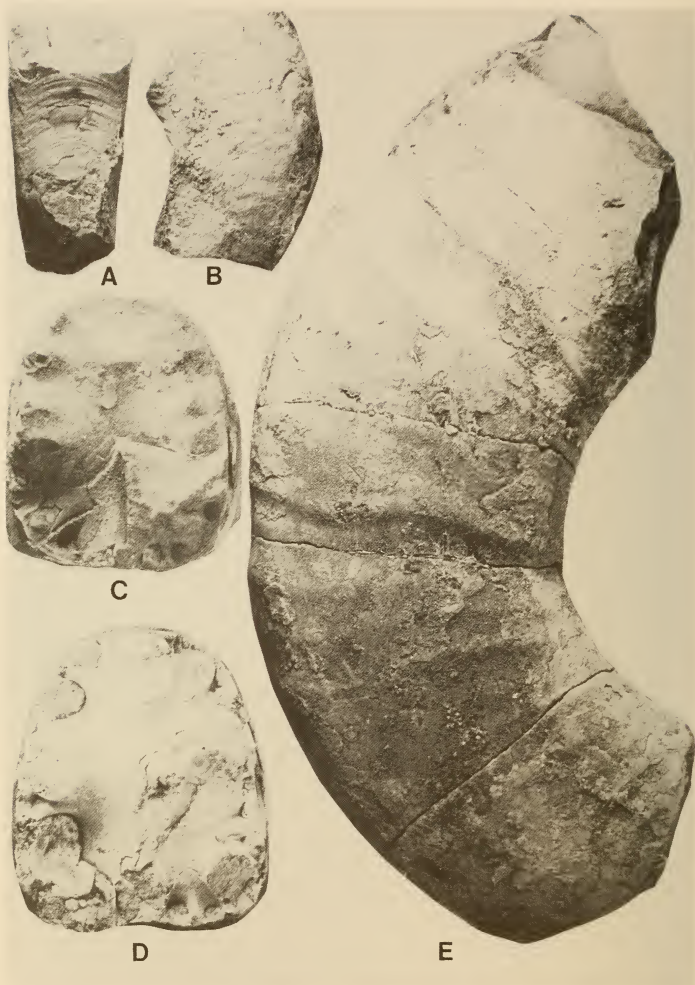


Fig. 21. *Crioceratites (C.) australis* sp. nov. A-B. BMNH C80040. C. BMNH C80041. D. BMNH C80049. E. BMNH C80035. Note dorsal zone of impression in A and distinct constrictions in E. All $\times 1$.



Fig. 22. *Crioceratites (C.) australis* sp. nov. A. BMNH C80046. B. BMNH C80047.
C. BMNH C80038. Note constriction in A and dorsal zone of impression in C.
All $\times 1$.



Fig. 23. *Crioceratites* (*C.*) *australis* sp. nov. A. BMNH C80047. B-C. Inner whorls of BMNH C80047. D. BMNH C80040. All $\times 1$.

Discussion

As in the case of *Crioceratites*, recent reviews of the group of small ancyloceratids, variously referred to as *Acrioceras*, *Aspinoceras*, *Paraspinoceras*, *Subaspinoceras*, *Mesocrioceras* or *Protacrioceras* by Sarkar (1955), Wiedmann (1962), Thomel (1964), Breskovski (1966), Dimitrova (1967), Kakabadze (1981), Thomel *et al.* (1987, 1990), and Vašíček & Michalík (1988), confuse rather than clarify taxonomic issues.

The most comprehensive discussion of the genus in the wider sense (as *Acrioceras* s.l.) is by Sarkar (1955) and, recently, in the restricted sense (as *Acrioceras* s.s.) is by Thomel *et al.* (1990).

Sarkar (1955) believed that *Acrioceras* could be divided into four subgenera, based primarily on the mode of coiling, i.e. acrioceratid or aspinoceratid, and whether major ribs, if present, are or are not trituberculate. His scheme is as follows:

1. *Acrioceras* s.s. Hyatt, 1900 (type species *Ancyloceras tabarelli* Astier, 1851: 19, pl. 7 (fig. 9))—coiling acrioceratid, major ribs trituberculate.
2. *Acrioceras* (*Paraspinoceras*) Breistroffer, 1952 (type species *Ancyloceras pulcherrimum* d'Orbigny, 1840: 495, pl. 121 (figs 3–7))—coiling acrioceratid, major ribs, if present, non-tuberculate; crozier *Hamulina*-like.
3. *Acrioceras* (*Aspinoceras*) Anderson, 1938 (type species *Aspinoceras hamlini* Anderson, 1938: 207, pl. 60 (figs 1–2))—coiling aspinoceratid, major ribs non-tuberculate.
4. *Acrioceras* (*Protacrioceras*) Sarkar, 1955 (type species *Ancyloceras ornatum* d'Orbigny, 1850: 101)—coiling aspinoceratid, major ribs trituberculate.

This classification has been modified to a greater or lesser extent by various subsequent authors.

Casey (1960: 18) did not regard *Aspinoceras* as an ancyloceratid, but rather saw it as a morphological type from which the '... Crioceratitidae and Heteroceratitidae may have diverged'. Wiedmann (1962: 143) only accepted *Acrioceras* s.s. and *A. (Aspinoceras)*, and regarded *Ancyloceras meriani* Ooster (1860: 35, pl. 39 (figs 1–7)) as a connecting link between these two subgenera. This view was followed by Immel (1978: 73) who pointed out that *Hamites phillipsi* Bean (in Phillips 1829, pl. 1 (fig. 30)), the type species of Spath's (1924: 78) genus *Hoplocrioceras*, is a typical example of *Aspinoceras*. According to the rules of priority, *A. (Aspinoceras)* should be regarded as a junior synonym of *A. (Hoplocrioceras)*. This view was followed by Kakabadze (1981) and recently also by Vašíček & Michalík (1988).

Thomel (1964) followed Sarkar's (1955) views, and later Thomel *et al.* (1987) added the genus *Subaspinoceras* (type species *Ancyloceras mulsanti* Astier, 1851: 18, pl. 6 (fig. 8)) for the European equivalents of the North American genus *Aspinoceras*.

Recently, Thomel *et al.* (1990) have clarified some of the problems surrounding *Acrioceras* s.s. on the basis of a large collection of specimens from the



Fig. 24. *Crioceratites (C.) australis* sp. nov. A. BMNH C80052. B. BMNH C80035. Both $\times 1$.

south-east of France. They are fully aware of the extreme intraspecific variation in *Acrioceras*, and that many of Sarkar's (1955) names are superfluous. Instead, they only consider six names sufficiently well understood to qualify as valid species in the biological sense. These include *Acrioceras meriani* (Ooster), *A. monopujaae* Sarkar, *A. ramkrishnai* Sarkar, *A. sarasini* Sarkar, *A. tabarelli* (Astier), and *A. terveri* (Astier).

Thomel *et al.* (1990) did not regard *Protacrioceras* as ancestral to *Acrioceras*; instead, they (p. 97) derived *Acrioceras* in the Upper Hauterivian (Zone of Sayni) from the group of *Paraspinoceras pulcherrimum*, via *Acrioceras meriani*. Two distinct acrioceratid lineages can be traced from *A. meriani*: (1) *A. meriani*–*A. tabarelli*–*A. terveri*, and (2) *A. sarasini*–*A. ramkrishnai*–*A. monopujaae*. In the former there is a distinct trend towards increase in size of the recurved hook in relation to the criocone whorls, but coiling remains more or less acrioceratid. In the latter lineage, especially in the Upper Barremian group of *A. monopujaae*, the shaft becomes incurved and the hook open, resulting in an aspinoceratid '*Protacrioceras*'-type of coiling.

Dimitrova's (1967) interpretation of *Protacrioceras* is unusual. *Protacrioceras tzankovi* (Dimitrova, 1967: 55, pl. 21 (fig. 1, 1a), pl. 22 (fig. 1)) is a gigantic ancyloceratid and certainly does not belong here in the sense of Sarkar (1955).

Epacrioceras Egoian, 1974 (type species *Epacrioceras rarum* Egoian, 1974: 225, figs 1–2), is an Upper Aptian homoeomorph of *Acrioceras*, thus far only known from the Western Caucasus. Ornament is virtually identical to that of *Acrioceras*, but the suture has a distinct bifid lateral lobe (L) in contrast to the trifid condition in *Acrioceras*.

Rawson (1975) suggested that *Acrioceras* and *Emericiceras*–*Paracrioceras* might be dimorphic. Details of this are discussed below (see p. 129).

Our Barremian material from Zululand shows that details of ornamentation are very variable but that, at specific level at least, acrioceratid and aspinoceratid coiled forms may be quite distinct, albeit possibly contemporary. All our specimens are tuberculate at some stage or other and are thus referred to *Acrioceras* s.s.

Occurrence

Acrioceras s.l. ranges from the Upper Hauterivian to the Upper Barremian, and occurs in both the Tethyan and Boreal realms. It is best known from West and Central Europe, but has also been recorded from the United States of America (California and Oregon) (Anderson 1938; Murphy 1975), Canada (Jeletzky 1964), Colombia (Etayo Serna 1968), Madagascar (Collignon 1962), Antarctica (Thomson 1974), Japan (Obata *et al.* 1976; Obata & Ogawa 1976), and Indonesia (as *Hoplocrioceras*—Skwarko & Thieuloy 1989).

Reports of *Acrioceras* from the Lower Aptian (*cf.* Wright 1957: L211; Drushchits & Kudryavtseva 1960: 294; Kakabadze 1981: 96) have to be viewed

with suspicion, as is discussed below (p. 129) in the section on dimorphism. Records from Australia (Kakabadze 1981: 96) cannot be confirmed.

Acrioceras (Acrioceras) zulu sp. nov.

Figs 25–28, 29A–B, ?C, 30A–D, ?E–F, 31A–D, ?E, ?F–J, 32B–C, 33–34, 39

Type. Holotype is BMNH C80009 from locality 170, cliff and gully sections 2 km north-west of the Mlambongwenya Trading Store, on the north side of the stream, Makatini Formation, Barremian I.

Material

Fifteen specimens: BMNH C80005a–c, C80006–80008, SAM–PCZ8423, PCZ8426, PCZ8428–8430, PCZ8440–1, PCZ8443, PCZ8449, PCZ8451 and PCZ8666, all from the same locality as the holotype; PCZ8441 is from Bed 25; PCZ8423 is from Bed 1.

Description

The shell is small, ancyloceratid, with an initial variably coiled spiral section, followed by a straight shaft. None of our specimens possesses a complete crozier, but PCZ8423 (Fig. 33A–B) shows part of a short hook, as does C80009 (Fig. 34), suggesting an overall length of c. 50 mm at maturity.

The earliest developmental stages are best seen in C80005c (Fig. 28A), and PCZ8443 (Fig. 30A–D). The former shows the globose protoconch 0,5 mm in diameter, in close contact with half a whorl of phragmocone. Coiling is very variable—open with the early whorls not in close contact in C80005c (Fig. 28A) and tight with the whorls in close contact in PCZ8443 (Fig. 30A–D). The whorl section of the early spiral varies from compressed in C80005c to depressed in PCZ8443 (Figs 28A, 30A–D). The dorsum is slightly concave.

Ornament on the spire and shaft is extremely variable. At one extreme, as represented by C80005c (Fig. 28A), a compressed individual, there are numerous (70–80) fine, delicate, flexuous ribs per whorl. Mere striae on the dorsum, they strengthen across the umbilical wall (where they are distinctly rectiradiate) and are concave across the umbilical shoulder. Most ribs are single, although a

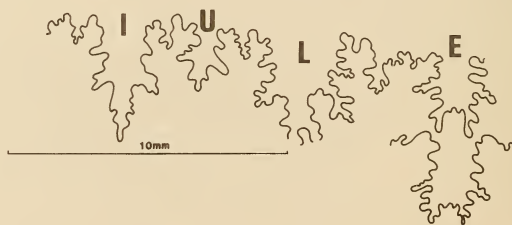


Fig. 25. *Acrioceras (A.) zulu* sp. nov. Suture line. SAM–PCZ8668.

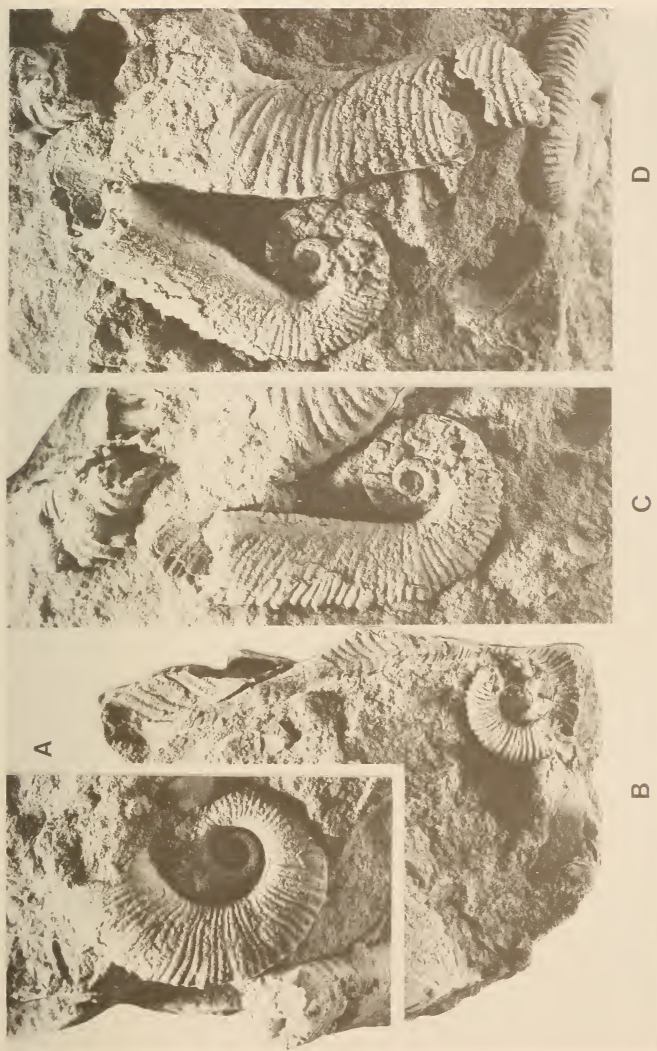


Fig. 26. *Actioceras (A.) zulu* sp. nov. A. BMNH C80005c. B. BMNH C80005b. C. BMNH C80005a. D. BMNH C80005a-b. Compare loose coiling in A with that in C and D. All $\times 2$.

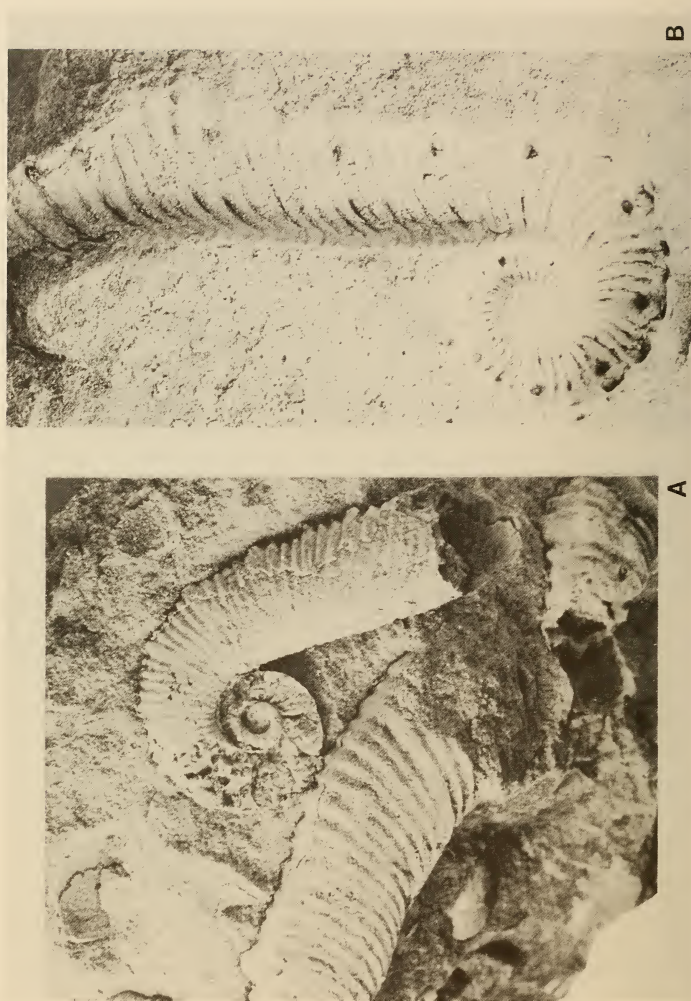


Fig. 27. *Acriceras* (A.) *zulu* sp. nov. A. BMNH C80005a-b. Specimens with weak, bituberculate ornament. B. Holotype, BMNH C80009. Both $\times 2$.

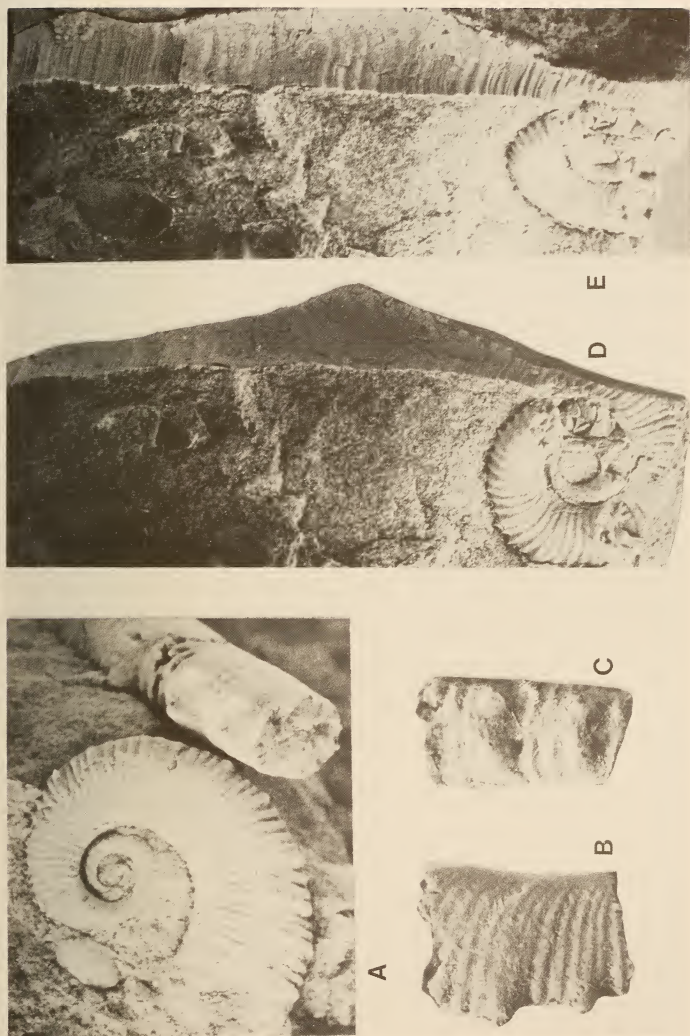


Fig. 28. *Actioceras* (A.) *zulu* sp. nov. A. BMNH C80005c. B-C. BMNH C80005b. D-E. BMNH C80005b. A-C $\times 2$; D-E $\times 3.5$.

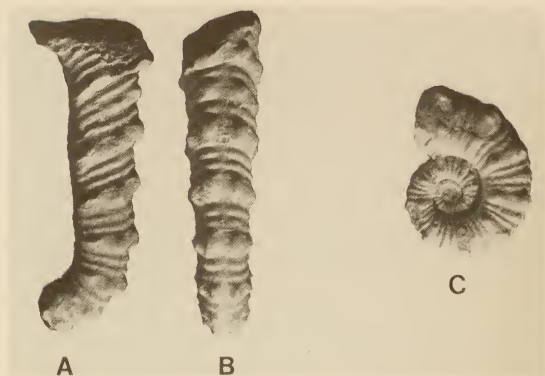


Fig. 29. A-B. *Acrioceras* (A.) *zulu* sp. nov. Coarsely ornamented, sextuberculate shaft. SAM-PCZ8666. C. Coarsely ornamented criocone whorls that could belong to either *Acrioceras* (A.) *zulu* sp. nov. or coarsely ornamented form of *Crioceratites* (C.) *yrigoyeni* (Leanza, 1970). SAM-PCZ8667. Both $\times 1$.

few branch into two or three at the shoulder. They are slightly prorsiradiate on the flanks, feebly convex on the inner flank, concave on the outer flank, and quite markedly projected on the ventrolateral shoulder. Narrow at the umbilicus, the ribs thicken and strengthen across the flanks. On some ribs there is a slight indication of strengthening at the lower ventrolateral position, although no clearly defined tubercle develops. In contrast, ventral, transversely elongated tubercles are well developed, and some bear indications that they are in fact the bases of short spines. Tubercle strength varies from mere swellings to marked, sharp excrescences. As size increases, there is a tendency towards a pattern of a strongly tuberculate rib followed by three to five weakly tuberculate ribs. In a few cases a pair of flank ribs connect to one of these more pronounced tubercles. All ribs are broad and low and feebly convex across the venter.

Less compressed forms, such as C80005a (Fig. 26C), are more robustly ribbed and with a distinct rursiradiate style and stronger suggestion of a lower ventrolateral tubercle. These specimens form a link to the coarsely ribbed form illustrated by C80009 (Fig. 27B) and PCZ8443 (Fig. 30A-D). In these, differentiation of ribbing occurs—the major ribs bearing variably developed umbilical tubercles, very strong ventrolateral and strong ventral tubercles.

This range of variation is also seen on the shafts of our specimens. In the compressed variety, ribbing is dense and prorsiradiate, and only ventral tubercles, linking two to three ribs, occur. On the more robustly ornamented specimens (Fig. 29A-B), differentiation of ribbing is more pronounced, and distinct umbilical, ventrolateral and ventral tubercles are developed. In some, e.g. PCZ8441 (Fig. 33C-D) every rib on the shaft is tuberculate.

Discussion

As here interpreted, this species is very variable, so much so that, in terms of ornament on the spiral whorls, we can speak of compressed, bi- or incipiently quadrituberculate, finely ribbed forms, e.g. C80005a-c (Fig. 26), 'normally' ornamented (C80009, Fig. 27B), and coarsely ornamented forms (PCZ8666, Fig. 29A-B). As far as the coiling of the spiral section is concerned, we can speak of tightly coiled ancyloceratid (C80005a, Fig. 26C), and loosely coiled aspinoceratid or crioceratitid forms (C80005c (Fig. 26A) and PCZ8451). As far as ornament on the shaft is concerned, we can distinguish bi- (C80005c, Fig. 28A), quadri- (C80008) and sextuberculate (PCZ8666, Fig. 29A-B) forms.

Variation is so extensive that virtually every specimen merits description as a separate species, if species concepts of most previous workers on this genus were applied (which is more or less what Sarkar (1955) did in his description of the French material).

Acrioceras zulu clearly belongs to the group of *Acrioceras tabarelli* (Astier, 1851: 19, pl. 7 (fig. 9)), but it connects morphologically with *Paraspinoceras pulcherrimum* (d'Orbigny, 1840: 495, pl. 121 (figs 3-7)) via the compressed, finely ribbed, bituberculate forms.

Acrioceras tabarelli is a very variable species, as noted by Thomel (1964: 41 'd'une forme tres plastique') and Thomel *et al.* (1990). Sarkar (1955: 102-112) tried to overcome this problem by naming virtually every individual specimen, e.g. *Acrioceras tabarelli* var. *sarasini*, var. *uhligi*, *Acrioceras* cf. *tabarelli* sp. forme nrs 1-8. Thomel *et al.* (1990) provided excellent figures to illustrate the wide extent of intraspecific variation in *A. tabarelli*. Even so, their extensive use of open nomenclature in the captions to their excellent figures clearly shows how difficult it is to put a definite specific or subspecific name to every specimen, even if it is completely preserved. Apart from two formal subspecific names, *A. tabarelli tabarelli* and *A. t. sugrivaï*, Thomel *et al.* (1990) used the following combination of names in the explanation to their figures:

Acrioceras aff. *tabarelli* (Astier)—pl. 2 (fig. 11).

Acrioceras gr. *tabarelli* (Astier)—pl. 3 (fig. 1), pl. 4 (figs 4-6), pl. 8 (fig. 7), pl. 9 (fig. 2).

Acrioceras gr. *tabarelli* (Astier) aff. *uhligi* Sarkar—pl. 3 (fig. 2).

Acrioceras entre *tabarelli* (Astier) et *sarasini* (Sarkar)—pl. 3 (figs 7-8), pl. 5 (fig. 6), pl. 9 (figs 3-4).

Acrioceras entre *sarasini* Sarkar et *tabarelli* (Astier)—pl. 4 (fig. 1), pl. 6 (figs 4-5).

Acrioceras entre *tabarelli* (Astier) et *terveri* (Astier)—pl. 4 (figs 8-9).

Acrioceras entre *tabarelli* (Astier)—*terveri* (Astier) et *uhligi* Sarkar—pl. 4 (fig. 10).

Acrioceras gr. *tabarelli* (Astier) comparer á *Acrioceras* cf. *tabarelli* Astier formes 4 et 5 de Sarkar—pl. 10 (fig. 4).

Acrioceras sp. entre gr. *tabarelli* (Astier) et *uhligi* Sarkar—pl. 11 (fig. 6).

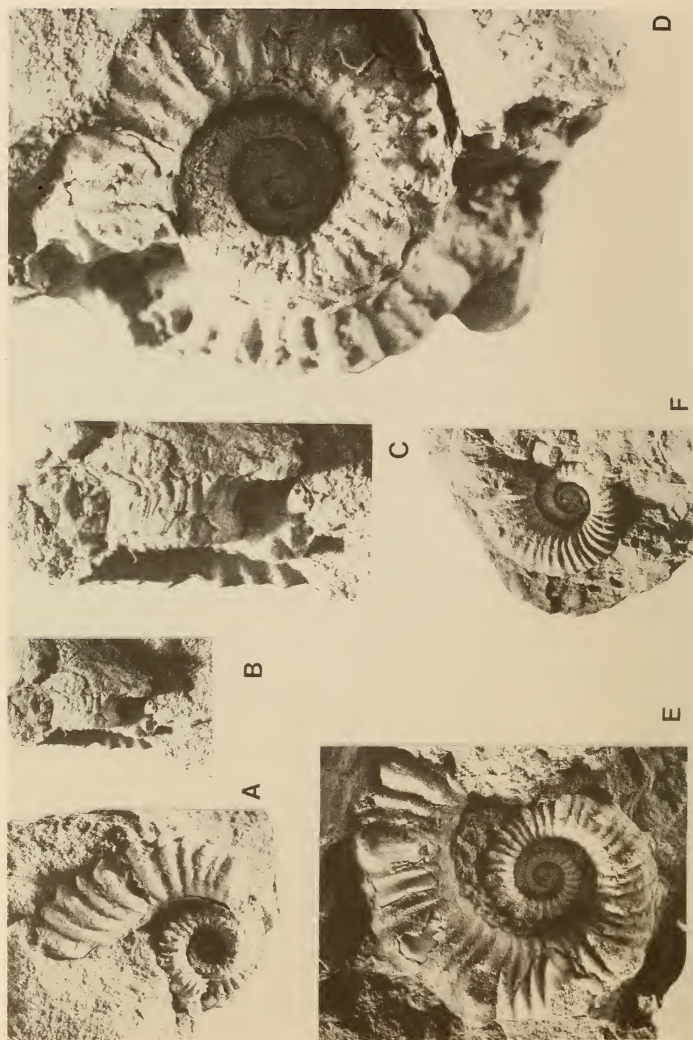


Fig. 30. A-D. *Acriceras* (A.) *zulu* sp. nov. SAM-PCZ8443. E-F. Early *Crioceratites* (C.) *yrigoyeni* (Leanza, 1970) or *Acriceras* (A.) *zulu* sp. nov. E. SAM-PCZ8447. F. BMNH C80007. A-B, E-F $\times 2$; C $\times 4$; D $\times 5$.

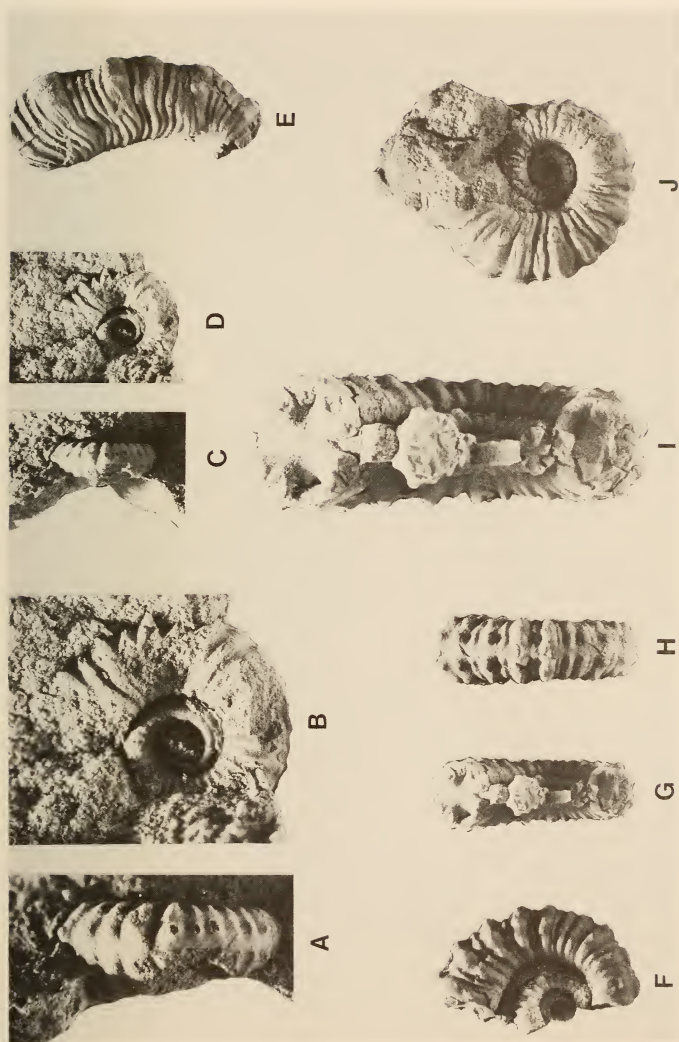


Fig. 31. A-D. Early eriocone whorls of *Acriceras* (A.) *zulu* sp. nov. SAM-PCZ8440. E. ?*Acriceras* (A.) *zulu* sp. nov. SAM-PCZ8430. F-J. Early acricone whorls of *Acriceras* (A.) *zulu* sp. nov. or *Crioceratites* (C.) *yrigoyeni* (Leanza, 1970). F-I. SAM-PCZ8425b. J. SAM-PCZ8433. A-B, I $\times 4$; C-H, J $\times 2$.

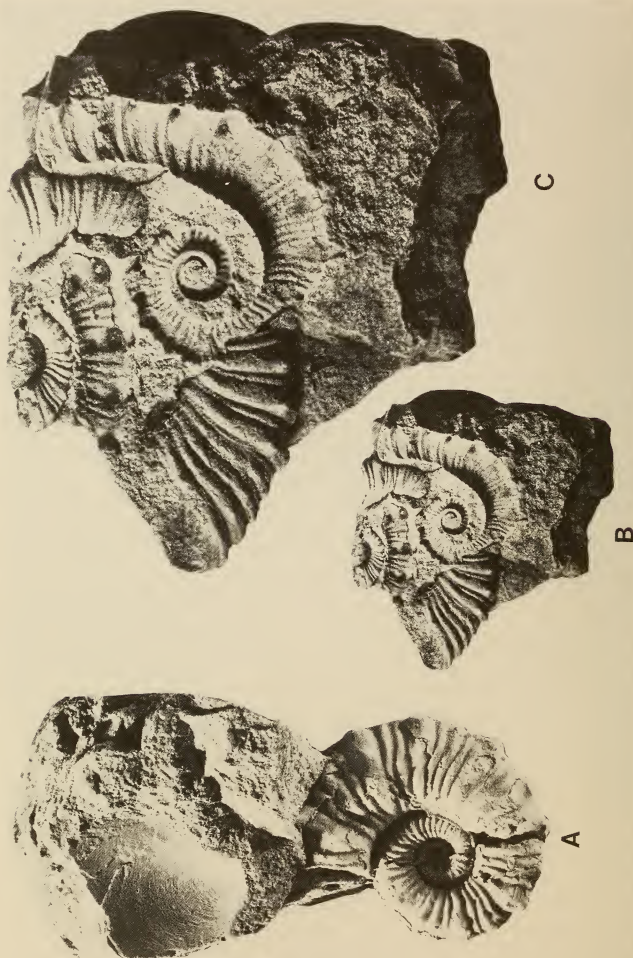


Fig. 32. A. *Crioceratites* (C.) *yrigoyeni* (Leanza, 1970). SAM-PCZ8424a-b. B-C. *Acriceras* (A.) *zulu* sp. nov. SAM-PCZ8669. A-C $\times 2$, B $\times 1$.



Fig. 33. *Acrioceras (A.) zulu* sp. nov. A-B. SAM-PCZ8423, specimen with part of final hook preserved. C-D. SAM-PCZ8441. Part of shaft with prominent sextuberculate ornament. Both $\times 2$.



Fig. 34. *Acrioceras* (*A.*) *zulu* sp. nov.
Silicone mould of holotype,
BMNH C80009.

None of the European specimens has quite as coarse ornamentation as our most strongly ornamented specimens; at the other extreme, none of the Zululand specimens is as finely ribbed and non-tuberculate as *Paraspinoceras pulcherrimum*. *Acrioceras* (*A.*) *zulu* ranges morphologically from coarsely ornamented, sextuberculate forms, much more coarsely ornamented than any specimens of *A. tabarelli* known, to finely ornamented, bi- or incipiently quadrituberculate forms, although never as finely ornamented as *Paraspinoceras pulcherrimum*.

According to Thomel *et al.* (1990), *Acrioceras tabarelli* is restricted to the Lower Barremian and *A. (Paraspinoceras) pulcherrimum* ranges through most of the Upper Hauterivian and Lower Barremian (Thomel 1964: 73, table 5). *Acrioceras zulu*, in contrast, is only known from the Upper Barremian of Zululand. Thus, on stratigraphic grounds alone, separation of *A. (A.) zulu* from *A. tabarelli* and *A. pulcherrimum* seems justifiable.

Acrioceras terveri (Astier, 1851) is a related Lower Barremian species that differs mainly in the strong development of the shaft and crozier in relation to the cricocone section. Some specimens of *A. terveri*, figured by Thomel *et al.* (1990, e.g. pl. 13 (fig. 1)), are as strongly ornamented as some of our specimens of *A. (A.) zulu* (e.g. Figs 29, 33).

Acrioceras monopujaee Sarkar, 1955, appears to be restricted to the Upper Barremian, according to Thomel *et al.* (1990). It is also very variable and

Thomel *et al.* (1990) recognized four different subspecies—*A. monopujaae monopujaae* Sarkar, 1955, *A. monopujaae minor* Thomel *et al.*, 1990, *A. m. multicoatum* Sarkar, 1955, and *A. m. yvanii* Thomel *et al.*, 1990. Coiling in *A. monopujaae* appears to be predominantly aspinoceratid (of the type of *Protacrioceras* in the sense of Sarkar 1955), compared to distinctly acrioceratid in *A. (A.) zulu*. This suffices to distinguish between the two species.

The criocone whorls of coarsely ornamented variants of *A. (A.) zulu* are indistinguishable from those of *Crioceratites (C.) yrigoyeni* (Leanza) (see p. 84). Implications of these similarities are discussed below (p. 129).

Occurrence

Upper Barremian (Barremian I–II) of Zululand.

Acrioceras sp.

Fig. 35

Material

A single specimen, SAM-PCZ8442, from the basal bed, Bed 1, at locality 170, cliff and gully sections 2 km north-west of Mlambongwenya Trading Store, on the north side of the stream. Makatini Formation, Barremian I.

Description

The specimen is about 45 mm long, and consists of part of the recurved crozier and an incomplete impression of the early whorls and succeeding curved shaft, partially preserved in sparry calcite.

The earliest whorls are smooth, with a rounded whorl section. They are followed by a stage with single ribbing and no visible lateral tuberculation. As far as can be seen, only ventral tubercles are developed on the coiled part of the phragmocone. At the end of the curved shaft, at or near the end of the phragmocone, a single pair of tubercles are visible on the venter.

Ornament on the rest of the recurved crozier consists of rounded, prorsiradiate ribs only, with no sign of tuberculation. The ribs arise on the umbilical wall, sweep forwards across the flanks, becoming progressively thicker towards the venter, and cross the latter without interruption. Some bifurcate at the umbilical edge.

Discussion

This species clearly differs from *Acrioceras (A.) zulu* in having a totally different mode of ornamentation, smaller size, and aspinoceratid, rather than acrioceratid coiling. Even though the criocone part is not fully preserved, that section is much smaller in relation to the rest of the shell than in *Acrioceras (A.) zulu*. This relationship is perhaps comparable to that of *Adouliceras* to *Ancyloceras* as far as general proportions are concerned.

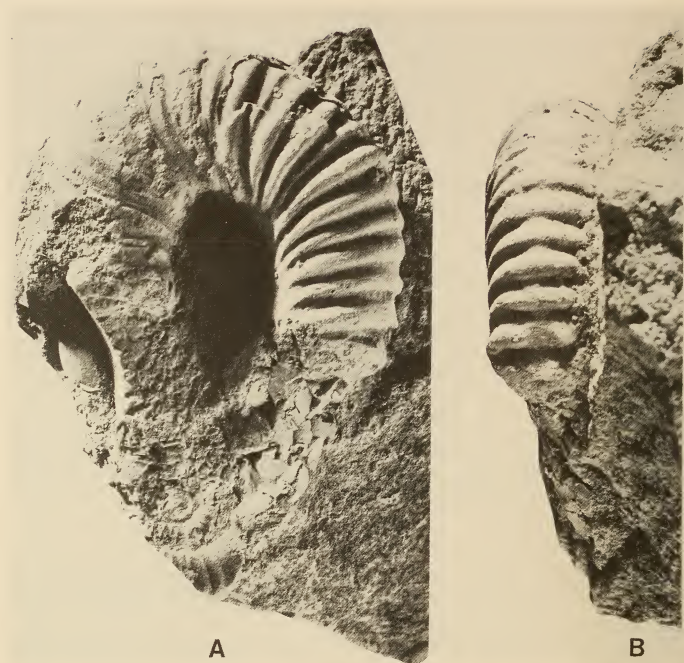


Fig. 35. *Acrioceras* sp. SAM-PCZ8442. $\times 2$.

Acrioceras (*Aspinoceras*) sp. aff. *brevis* (d'Orbigny) in Thomel (1964: 48, pl. 7 (fig. 11)) is very similar in overall shape, but the French specimen lacks tubercles.

Protacrioceras hourcqi Collignon (1962: 95, pl. 214 (figs 936–7)) from the Barremian of Antsalova, Madagascar, has coiling and relative proportions similar to our specimen, but has a trituberculate phragmocone. Given more material, it may be possible to connect our bituberculate specimen to the sextuberculate Malagasy specimen, very much in the same way as shown by the range of variation in *Acrioceras* (*A.*) *zulu*. For the present, a specific identification of the Zululand specimen is not possible.

Occurrence

Upper Barremian (Barremian I) of Zululand.

INCERTAE SEDIS

Genus *Hemihoplites* Spath, 1924[= *Matheronites* Renngarten, 1926]

Type species. Ammonites feraudinaus d'Orbigny, 1841, by original designation of Spath (1924: 84).

Discussion

Two specimens in our collections can be tentatively identified with material from Patagonia, described recently by Riccardi & Aguirre Urreta (1989) under the generic name of *Hemihoplites* Spath, 1924. Our material does not contribute in any constructive way to the discussion of whether *Hemihoplites* should be retained in a separate family Hemihoplitidae Spath, 1924, as proposed by Wright (1957, 1981) and followed by Riccardi & Aguirre Urreta (1989), or whether it in fact should be regarded as a recoiled crioceratitid, and included in the family Ancyloceratidae, as suggested by Wiedmann (1962, 1966) (see also Bogdanova 1971). We consequently refer our material to the genus *Hemihoplites* but leave the allocation at family level open.

Occurrence

According to Riccardi & Aguirre Urreta (1989), material that could be referred to *Hemihoplites* has been described from the Barremian and/or Lower Aptian of Mallorca, France, Italy, Bulgaria, Yugoslavia, Caucasus and Crimea, and questionably Mexico (Imlay 1938) and Canada. In southern Patagonia, *Hemihoplites* occurs in the Hauterivian and Barremian. Skwarko & Thieuloy (1989) recently described *Hemihoplites* from Indonesia.

Hemihoplites sp. cf. *H. ploszkiewiczzi* Riccardi & Aguirre Urreta, 1989

Figs 36A–B, 37, 38

Compare:

Hemihoplites ploszkiewiczzi Riccardi & Aguirre Urreta, 1989: 458, pl. 52 (figs 4–9), text-figs 3d–e, 5g–h, 6.

Material

BMNH C80033, from locality 170, cliff and gully sections, 2 km north-west of Mlambongwenya Trading Store, on the north side of the stream, Makatini Formation, Barremian I.

Description

The specimen is a wholly septate fragment with a maximum whorl height of 31 mm. Coiling appears to have been moderately evolute, with a deep, narrow, impressed dorsum (Fig. 38). The whorl section is compressed, with an estimated whorl breadth to height ratio of 0.5. The umbilical wall is quite low, flat and

sloping; the umbilical shoulder is abruptly rounded, the flanks flattened and convergent, shoulders bluntly rounded, and the venter narrow and broadly rounded. The greatest breadth is close to the umbilical shoulder.

Ornament consists of low, narrow, dense, crowded, rounded ribs. On the preserved fragment, nine ribs extend to the umbilicus, where they are low and wide. They sweep forwards to a point below midflank, where they split into two, rarely three, with an occasional intercalated rib, so that there are more ribs on the outer flank than on the inner. At the point of splitting, the ribs flex backwards, and are convex across the middle of the flanks, concave on the outer flank, and strongly projected on the ventrolateral shoulders. The ribs pass straight across the venter, weakening to the point of virtual effacement over the siphonal line.

The sutures are deeply and intricately incised (Fig. 37). The external lobe (E) is broad, with narrow incisions and a prominent median element; the lateral lobe (L) is large and asymmetrically trifid; the umbilical lobe (U) is small and imperfectly exposed; E/L is broad and asymmetrically bifid; and L/U is smaller and more symmetrically bifid.

Discussion

Our specimen resembles *Hemihoplites ploszkiewiczzi* Riccardi & Aguirre Urreta, 1989, from the Hauterivian of Patagonia, as far as the flexuous ribbing is concerned, but differs in being much more compressed ($Wb/Wh = 0,5$ compared to $0,8$). Given more material it may prove to be a new species.

We initially thought that this specimen might be a relatively late, closely coiled *Pseudothurmannia*, perhaps allied to *C. (P.) angulicostata* (d'Orbigny, 1840) (see e.g. Lapeyre 1974: 82, pl. 1 (figs 1–9)), *C. (P.) balearis* (Nolan, 1894) (see e.g. Wiedmann 1962: 128, pl. 8 (fig. 5), pl. 9 (fig. 1)), or *C. (P.) mortilleti* (Pictet & Loriol, 1858) (see e.g. Wiedmann 1962: 132, pl. 7 (fig. 5); Sornay 1968: 4, pl. 1 (fig. 1), text-fig. 1). In all these *C. (Pseudothurmannia)* species, however, some of the ribs arise in groups from elongated umbilical nodes on the outer whorls. These are lacking in the present specimen and we provisionally accept Riccardi & Aguirre Urreta's (1989) allocation of the material to *Hemihoplites*.

Occurrence

Barremian I of Zululand.

Hemihoplites sp. cf. *H. varicostatus* Riccardi & Aguirre Urreta, 1989

Fig. 36C–E

Compare:

Hemihoplites varicostatus Riccardi & Aguirre Urreta, 1989: 452, pl. 51 (figs 1–9), pl. 52 (figs 1–3), text-figs 3a–c, 4, 5a–f.

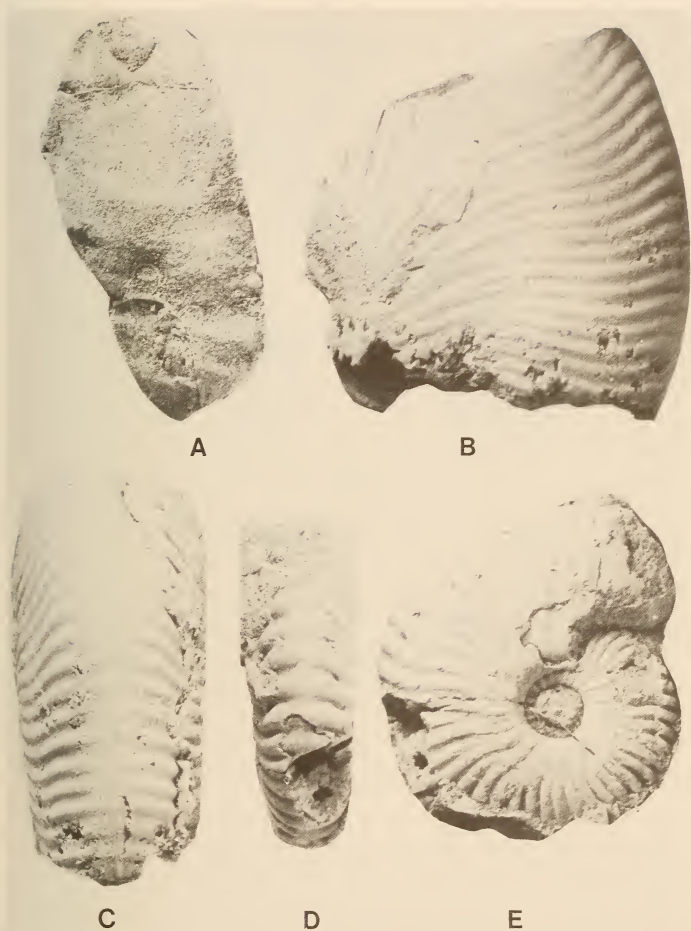


Fig. 36. A-B. *Hemihoplites* sp. cf. *H. ploszkiewiczzi* Riccardi & Aguirre Urreta, 1989. BMNH C80033. C-E. *Hemihoplites* sp. cf. *H. varicostatus* Riccardi & Aguirre Urreta, 1989. BMNH C80034. Both $\times 2$.

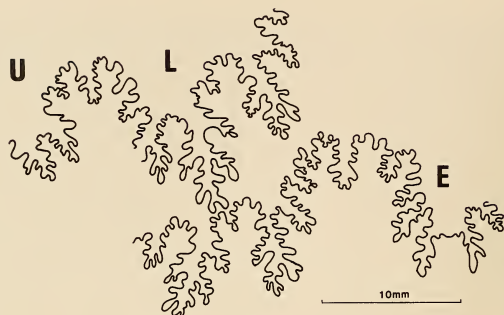


Fig. 37. *Hemihoplites* sp. cf. *H. ploszkiewiczzi* Riccardi & Aguirre Urreta, 1989.
Suture line of BMNH C80033.

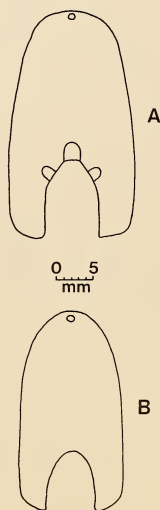


Fig. 38. *Hemihoplites* sp. cf. *H. ploszkiewiczzi*
Riccardi & Aguirre Urreta, 1989. Whorl
section of BMNH C80033.

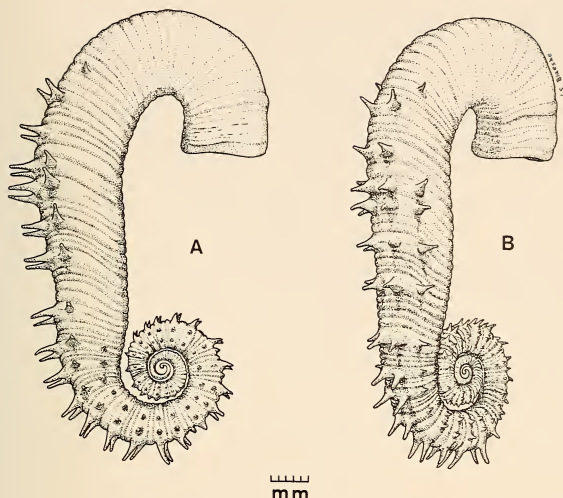


Fig. 39. Reconstruction of *Acrioceras* (*A.*) *zulu* sp. nov.

Material

One specimen only, BMNH C80034 from locality 170, cliff and gully sections, 2 km north-west of Mlambongwenya Trading Store, on the north side of the stream, Makatini Formation, Barremian I.

Dimensions

Specimen	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>
C80034	26,5	8,4 (32)	12,5 (47)	0,67	5,2 (20)

Description

The specimen is beautifully preserved, retaining replaced shell and part of the body chamber. Coiling is involute, with a small, shallow umbilicus (20% of the diameter). The umbilical wall is flat, and inclined outwards; the umbilical shoulder is abruptly rounded. The whorl section is compressed (whorl breadth to height ratio is 0,67), with the greatest breadth below midflank. The inner flanks are gently rounded, the outer flanks flattened and convergent, the ventro-lateral shoulders rounded and the rather narrow venter somewhat flattened.

Ornament consists of dense, broad, relatively strong, flexuous crowded ribs. Twenty-four ribs per whorl arise at the umbilical seam as mere striae. They are prorsiradiate across the umbilical wall and strengthen into feeble bullae at the

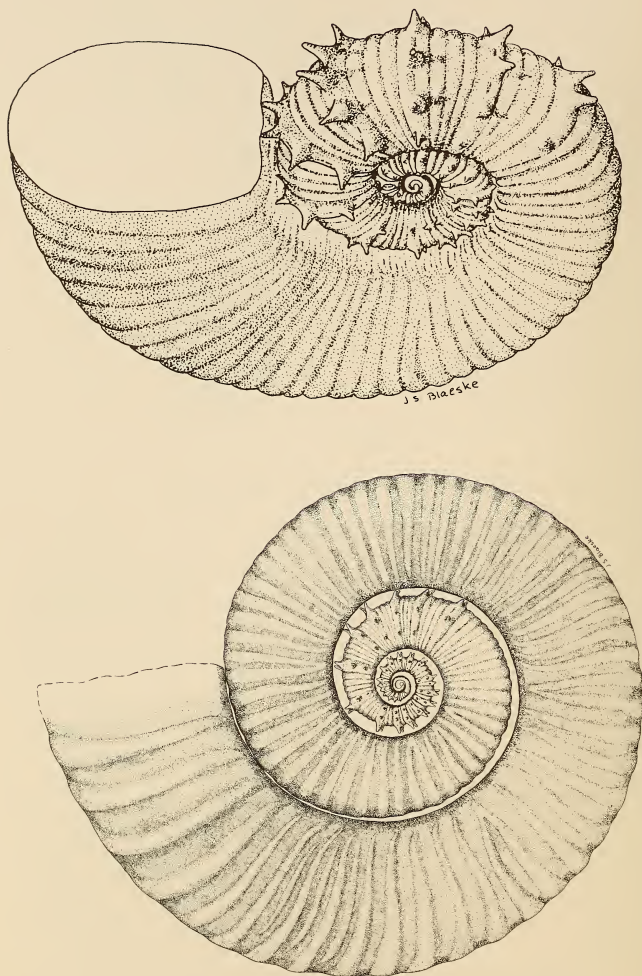


Fig. 40. Reconstruction of *Crioceratites* (*C.*) *yrigoyeni* (Leanza, 1970).

umbilical shoulder. On the flank, the ribs are at first narrow and prorsiradial; they split into pairs below midflank, with occasional ribs intercalated, giving a total of perhaps 40–50 ribs per whorl on the outer flank. The ribs are convex across the midflank and concave on the outer flank, and cross the venter with a distinct forward flexure and ventral convexity. Initially weak, the ribs strengthen and broaden from inner flank to ventrolateral shoulder, although weakening and broadening over the siphonal line.

The sutures are not exposed.

Discussion

Our specimen resembles the juvenile specimens of *Hemihoplites varicostatus* Riccardi & Aguirre Urreta, figured by Riccardi & Aguirre Urreta (1989, text-fig. 5a–f) as far as ornament is concerned, but differs in being much more involute. The umbilical diameter of the Patagonian specimens ranges from 28 to 40 per cent of the total diameter, compared to only 20 per cent in the Zululand specimen. For the present it is best to refer to the specimen as *Hemihoplites* sp. cf. *H. varicostatus*.

Superficially similar material has recently been recorded from Indonesia (Skwarko & Thieuloy 1989: 31, pl. 4 (figs 2–4)) as *Hemihoplites taminabuanensis*, where it is dated as early Barremian.

Hemihoplites sp. cf. *H. varicostatus* differs from *H. sp. cf. H. ploszkiewiczii* (see p. 123) in its coarser ribbing, especially the blunt ventral development of the ribs, as well as the presence of feeble bullae. Given a larger suite of specimens, these two individuals might prove to be different developmental stages or variants of the same species.

Occurrence

Barremian I of Zululand.

DISCUSSION ON SHELL SHAPE, DIMORPHISM AND SYSTEMATICS IN CRIOCERATITINAE AND ANCYCLOCERATINAE

Rawson (1975: 282) suggested that Ancyloceratidae with ancyloceratid/aspionoceratid coiling (herein referred to as acrioceratid), and larger, crioceratid forms might be dimorphic. Related to this, he observed that:

1. Spath (1924) grouped large crioceratid and smaller aspinoceratid forms in one genus—*Hoplocrioceras*; this cuts across normal taxonomic procedure of separating forms with different coiling.
2. Thomel (1964) pointed to the similarity between the ontogeny and ornamentation of some Tethyan crioceratitids and acrioceratids.
3. The type species of *Paracrioceras* is associated with body chambers of *Acrioceras* in the English Snettisham Clay (of the Boreal Realm)—a situation comparable to that found in Tethyan faunas as described by Thomel (1964).

Spath's (1924) observations may be ignored, because they are subjective, personal taxonomic views. If Spath really intended uniting forms with different coiling, it was certainly not with dimorphism in mind.

Thomel (1981) subsequently added to his initial views, commenting on the similarity between *Acrioceras tabarelli* (Astier) and *Emericiceras ottohaasi* Sarkar, and *Paraspinoceras dilatatum* (d'Orbigny) and *Crioceratites duvali* Leveillé, respectively, but he never actually referred to it as a manifestation of dimorphism.

Immel (1978: 28), in his revision of the Hauterivian-Barremian *Crioceratitinae*, totally ignored the issue of dimorphism, but disagreed with Spath's (1924) views that forms with aspinoceratid and crioceratitid coiling should be referred to the same genus (*Hoplocrioceras*). Immel made his views on dimorphism in general quite clear in a recent discussion (Immel 1987); this may explain the total omission of the subject in his (1978) work on the *Crioceratitinae*. Kaka-badze (1981: 75–76) referred to Rawson's (1975) statement, but regarded the similarities in early whorls of acrioceratid/aspinoceratid and crioceratitid forms as being due to 'phylogenetic proximity', rather than dimorphism.

Surprisingly enough, Thomel *et al.* (1990) scarcely touched on the topic of dimorphism in their monographic treatment of *Acrioceras* from the south-east of France. In the morphometric analysis of *Acrioceras*, they only referred briefly to dimorphism (p. 49) without any in-depth discussion.

In Zululand, *Crioceratites* (*C.*) *yrigoyeni* (Leanza) and *C. (C.) australis* were found at the same locality as *Acrioceras* (*A.*) *zulu* and *Acrioceras* sp. As we have noted above in the systematic descriptions, the inner whorls of *Crioceratites* (*C.*) *yrigoyeni* are indistinguishable from the spiral whorls of coarsely ornamented variants of *Acrioceras* (*A.*) *zulu*. Some of these specimens also occur together in the same nodules. It would be tempting to further link *Crioceratites* (*C.*) *australis* with the finely ribbed variants of *Acrioceras* (*A.*) *zulu* as a dimorphic pair. In fact, part of a finely ribbed fragment of *Acrioceras* (*A.*) *zulu* is preserved in BMNH C80046 (Fig. 20), a body chamber fragment of *Crioceratites* (*C.*) *australis*. But if we accept these as a dimorphic pair, it would mean formally separating finely and coarsely ribbed *Acrioceras* (*A.*) *zulu*. On purely morphological grounds, separation of finely and coarsely ribbed *Acrioceras* (*A.*) *zulu* is difficult, because of the presence of transitional forms, but not impossible. At present, our knowledge of the total range of variation of the inner whorls of *C. (C.) australis* is restricted to the holotype. However, the possible dimorphic association of finely ribbed *Acrioceras* (*A.*) *zulu* with *Crioceratites* (*C.*) *australis* may justify formal separation of these from coarsely ribbed *Acrioceras* (*A.*) *zulu*. Another alternative might be to link *C. (C.) australis* with *Acrioceras* sp.—an association substantiated by the co-occurrence of only two specimens—the holotype of *C. (C.) australis* and *Acrioceras* sp. in the basal bed (Bed 1) at locality 170.

The association of, and the morphological similarity between, the early whorls of Zululand representatives of *Acrioceras* and *Crioceratites* ('*Cryptocrio-*

ceras') suggest that it is possible, or probable, that they constitute a dimorphic pair. This association is analogous to that of *Acrioceras*–'Emericiceras' in the Tethyan Realm, and *Acrioceras*–'Paracrioceras' in the Boreal Realm.

A full discussion on dimorphism in the subfamilies Crioceratitinae and Ancyloceratinae should be based on precisely located material from the classic European localities in the Boreal and Tethyan realms, respectively. We here limit ourselves to a discussion of some obvious taxonomic implications of the recognition of possible dimorphism in the Crioceratitinae and Ancyloceratinae.

Taxonomic implications

If the association of *Acrioceras*–'Emericiceras' in the Tethyan Realm, *Acrioceras*–'Paracrioceras' in the Boreal Realm, and *Acrioceras*–'Cryptocrioceras' in Zululand, respectively, is due to dimorphism, it would suggest a rather complicated social life for *Acrioceras* with three different, geographically separated sexual counterparts. Either *Acrioceras* has to be split into three different supra-specific taxa, one for each biogeographically distinct dimorphic partner, or 'Emericiceras', 'Paracrioceras' and 'Cryptocrioceras' have to be regarded as synonyms.

There do appear to be differences between Tethyan and Boreal *Acrioceras*. Subsurface material from Salzgitter, Federal German Republic, described by Immel (1978, pl. 6 (fig. 5)) as *Acrioceras* gr. ex. *A. tabarelli* (see also Immel 1979a: 136), differs from the typical Tethyan species, but these differences are not sufficient for generic separation. It rather seems to suggest that the differences between Boreal and Tethyan *Acrioceras* might be analogous, or of the same order as those between 'Paracrioceras' and 'Emericiceras'.

From a phylogenetic point of view, there are no serious objections to uniting (Boreal and Tethyan) 'Paracrioceras' and 'Emericiceras', and regarding them as synonyms or, at most, as a subgenus of *Crioceratites*. Kemper *et al.* (1981), in fact, refuted Immel's (1978) views that the north-west European and Tethyan crioceratid faunas are specifically distinct.

The association of 'Cryptocrioceras' with *Acrioceras* in Zululand lends support to Thomel's (1964: 419) objection that 'Sornayites' (of which 'Cryptocrioceras' is a possible junior objective synonym) need not be separated formally from *Crioceratites* s.s. If that is the case, 'Paracrioceras', 'Emericiceras' and 'Sornayites' ('Cryptocrioceras') can all be regarded as synonyms. If separation of these (predominantly strongly tuberculate on the inner whorls) Barremian species from *Crioceratites* at subgeneric level is required, the oldest name, *Paracrioceras* Spath, 1924, has priority.

If *Acrioceras* s.l. and the 'Paracrioceras'–'Emericiceras'–'Cryptocrioceras' part of *Crioceratites* are indeed dimorphs, it would be untenable to place *Acrioceras* s.l. and *Crioceratites* into different subfamilies (Crioceratitinae, Ancyloceratinae, Helicancyliinae) as is current practice (*cf.* Wright 1957; Aguirre Urreta 1986) and taken to extremes by Dimitrova (1970).

From a taxonomic point of view, the recognition of *Acrioceras* s.l. and the '*Paracrioceras*–*Emericiceras*–*Cryptocrioceras*' lineage of *Crioceratites* as a dimorphic pair would certainly make sense. To prove it is difficult on the basis of the present material; we need more stratigraphically substantiated records on the co-occurrence of crioceratitid and ancyloceratid forms with similar early whorls. We doubt if the name *Acrioceras* will ever disappear from common use—but the confirmation that it is the dimorphic partner of *Crioceratites* will confirm the futility of referring them to two different subfamilies.

CONCLUSION

From the above discussion it appears likely, or even probable, that small forms with acrioceratid/aspinoceratid coiling (*Acrioceras*) and larger forms with crioceratitid coiling (*Crioceratites*) might constitute a dimorphic pair in the family Ancyloceratidae. From a systematic point of view, this hypothesis is very attractive, because it would unambiguously clear the way for uniting the subfamilies Crioceratitinae and Ancyloceratinae, and would further simplify the systematics of the '*Paracrioceras*–*Emericiceras*–*Cryptocrioceras*' plexus by removing the traditional Boreal, Tethyan and Gondwanid geographic taxonomic barriers.

However, because there is an element of uncertainty, we retain the names *Acrioceras* and *Crioceratites* in the systematic description. But, being aware of their possible dimorphic association with *Acrioceras*, there is no justification for maintaining *Paracrioceras*, *Emericiceras* or *Cryptocrioceras* separate from each other or from *Crioceratites* s.s.; neither is separation into two subfamilies, Ancyloceratinae and Crioceratitinae (as here reluctantly employed for taxonomic 'tidiness') justifiable.

ACKNOWLEDGEMENTS

Financial aid from the Foundation for Research Development (South Africa) (FRD) to Klinger, and the National Environment Research Council (NERC) to Kennedy, is gratefully acknowledged. For discussions, advice and literature we thank Drs M. B. Aguirre Urreta (Buenos Aires), H. Immel (Munich), M. V. Kakabadze (Tbilisi), and G. Thomel (Saint-Martin-du-var), but we accept responsibility for the opinions expressed here. Thanks are due to Jacqueline Blaeske, Sally Dove and Madel Joubert (South African Museum) for technical assistance.

REFERENCES

- AGUIRRE URRETA, M. B. 1981. In: AGUIRRE URRETA, M. B. & RAMOS, V. A. Estratigrafía y paleontología de la Alta Cuenca del Río Roble Cordillera Patagónica—Provincia de Santa Cruz. *Actas. VII Congreso Geológico Argentino, 20–26 septiembre 1981, San Luis* 3: 101–148.

- AGUIRRE URRETA, M. B. 1986. Aptian ammonites from the Argentinian Austral Basin. The subfamily Helicancylinae Hyatt, 1894. *Annals of the South African Museum* **96** (7): 271-314.
- AGUIRRE URRETA, M. B. & KLINGER, H. C. 1986. Upper Barremian Heteroceratinae (Cephalopoda, Ammonoidea) from Patagonia and Zululand, with comments on the systematics of the subfamily. *Annals of the South African Museum* **96** (8): 315-358.
- ANDERSON, F. M. 1938. Lower Cretaceous deposits in California and Oregon. *Special Papers of the Geological Society of America* **16**: 1-339.
- ASTIER, J. E. 1851. Catalog descriptif des *Ancyloceras* appartenant à l'étage néocomien d'Escagnolles et des Basses-Alpes. *Annales des sciences physiques et Naturelles d'Agriculture et d'Industrie* **3**: 435-456.
- BATSEVICH, L. F. & SIMONOVICH, S. E. 1873. Geologicheskoe opisanie chasti kutaïskogo uezda, Kutaïsskoi gubernii, izvestnoi pod imenem Okriba. *Materialy dlya geologii Kavkaza*.
- BLASCO, G., NULLO, F. E. & PLOSKIEWICZ, J. 1980. El género *Colchidites* Djanéldzé, 1926 y la posición estratigráfica del género *Hatchericeras* Stanton, 1901 en la Estancia Tucú-Tucú, Provincia de Santa Cruz. *Revista de la Asociación geológica argentina* **35** (1): 41-58.
- BOGDANOVA, T. N. 1971. New Barremian ammonites from Western Turkmenia. *Paleontological Journal* **3**: 334-344.
- BREISTROFFER, M. 1947. Notes de Nomenclature paleozoologique. *Procès-verbaux de la Société dauphinoise d'études biologiques et de protection de la nature* **26**: 1-5.
- BREISTROFFER, M. 1952. Sur la position systématique du genre *Ptychoceras* D'Orb. *Travaux du Laboratoire de géologie de la Faculté des sciences de l'Université de Grenoble* **29**: 47-54.
- BRESKOVSKI, S. 1966. Biostratigrafija na barema juzhno ot selo Brestok, Varnensko. *Trudove vurkhu geologiyata na Bulgariya. Sofia (Palaeontologiya)* **8**: 71-121.
- BUSNARDO, R. 1970. Les *Pseudothurmannia* (Ammonoidea) de l'Hauterivien Supérieur de la Montagne de Lure. *Documents du Laboratoire de géologie de la Faculté des sciences de Lyon* **37**: 133-145.
- CAMACHO, H. & RICCARDI, A. C. 1978. Invertebrados. Megafauna. VII Congreso Geológico Argentino. 9-15 April 1978, Neuquén: 137-144.
- CASEY, R. C. 1960. The Ammonoidea of the Lower Greensand. Part I. *Monographs. Palaeontographical Society*: 1-44.
- CASEY, R. C. 1961. The Ammonoidea of the Lower Greensand. Part 2. *Monographs. Palaeontographical Society* **114**: 45-118.
- COLLIGNON, M. 1949. Faune Néocomienne des couches à criocères de Belohasifaka (Cercle de Sitampiky) (Madagascar). *Annales géologiques du Service des mines, Madagascar* **15**: 55-83.
- COLLIGNON, M. 1962. Atlas des fossiles caractéristiques de Madagascar (Ammonites). VIII. (Berriasien, Valanginien, Hauterivien, Barremien). Tananarive: Service Géologique.
- COTTEAU, J. 1937. Types du Prodrome de Paléontologie stratigraphique universelle de d'Orbigny, B.-Néocomien supérieur ou Urgonien. *Annales de paléontologie* **26** (1): 17-48.
- DIMITROVA, N. 1967. Les fossiles de Bulgarie. IV. Crétacé inférieur. Cephalopoda (Nauti-loidea et Ammonoidea). *Izvestiya na Geologicheskaya Institut, Bulgarska Akademiya na Naukite, Sofiya (Palaeontologiya)* **4**: 1-424.
- DIMITROVA, N. 1970. Phylogénèse des ammonites hétéromorphes du Crétacé inférieur. *Izvestiya na Geologicheskaya Institut, Bulgarska Akademiya na Naukite, Sofiya (Palaeontologiya)* **19**: 71-110.
- DOUVILLÉ, H. 1916. Les terrains secondaires dans le massif du Moghara à l'est de l'isthme de Suez. *Mémoires de l'Académie des sciences de l'Institut de France* **54**: 1-184.
- DRUSHCHITS, V. V. & KUDRYAVTSEV, M. Ts. 1960. Ammonitiy. In: *Atlas niznemelovoy fauny Severnogo Kavkaza i Kryma. Trudy Vsesojuz institut gazovoj* **1960**: 249-355.
- EGOIAN, V. L. 1974. A new family of loosely coiled ammonites from the Aptian deposits in the Western Caucasus. *Doklady Akademii nauk SSSR (Earth Science Sections)* **217** (1-6): 223-226.
- ETAYO SERNA, F. 1968. Apuntaciones acerca de algunas amonitas interesantes del Hauteriviano y del Barremiano del region de Villa de Leiva (Boyaca, Colombia, S.A.). *Boletín de geología, Facultad de petróleos, Universidad industrial de Santander* **24**: 51-70.

- FÖRSTER, R. 1975. Die geologische Entwicklung von Süd-Mozambique seit der Unterkreide und die Ammoniten-Fauna von Unterkreide und Cenoman. *Geologisches Jahrbuch* (B) 12: 3-324.
- GERHARDT, K. 1897. Beitrag zur Geologie und Palaeontologie von Südamerika. V. Beitrag zur Kenntnis der Kreideformation in Venezuela und Peru. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* (Beilageband) 11: 5-208.
- GERTH, H. 1925. La fauna Neocomiana de la Cordillera Argentina en la parte meridional de la provincia de Mendoza. *Actas de la Academia nacional de ciencias en Cordoba* 9 (2): 57-132.
- GILL, T. 1871. Arrangement of the families of Mollusks. *Smithsonian Miscellaneous Collections* 227: 1-49.
- GIOVINE, A. T. Y. 1950. Algunos cefalópodos del Hauterivense de Neuquén. *Revista de la Asociación geológica argentina* 5 (2): 35-76.
- GIOVINE, A. T. Y. 1952. Sobre una nueva especie de *Criocerat*. *Revista de la Asociación geológica argentina* 7 (1): 71-75.
- HONNORAT-BASTIDE, E. F. 1889. Formes nouvelles d'Ammonites de Belemnites et de *Criocerat*. *Compte rendu de l'Association française pour l'avancement des sciences* 2: 462-466.
- HYATT, A. 1894. Phylogeny of an acquired characteristic. *Proceedings of the American Philosophical Society* 32: 349-647.
- HYATT, A. 1900. Cephalopoda. In: EASTMAN, C. R. transl. *Text-book of palaeontology*, by Karl A. von Zittel 1: 502-604. London: Macmillan & Co.
- IMLAY, R. W. 1938. Ammonites of the Taraises Formation of northern Mexico. *Bulletin of the Geological Society of America* 49: 539-602.
- IMMEL, H. 1978. *Crioceratiten* (Ancyloceratina, Ammonoidea) des mediterranen und borealen Hauterive-Barreme (Unterkreide). *Palaeontographica* (A) 163 (1-3): 1-85.
- IMMEL, H. 1979a. Die Ammonitengliederung des mediterranen und borealen Hauterive und Barreme unter besonderer Berücksichtigung heteromorpher Ammoniten der Gattung *Crioceratites* Leveillé. *Newsletters on Stratigraphy* 7 (3): 121-141.
- IMMEL, H. 1979b. Über den Ursprung der borealen *Crioceratiten* und zur Phylogenie der Gattung *Crioceratites* Leveillé (Ammonoidea, Kreide). *Aspekte der Kreide Europas*. *IUGS* (Series A) 6: 129-140.
- IMMEL, H. 1987. Die Kreideammoniten der nördlichen Kalkalpen. *Zitteliana* 15: 3-163.
- JELETKY, J. A. 1964. Illustrations of Canadian fossils. Lower Cretaceous marine index fossils of the sedimentary basins of western and arctic Canada. *Geological Survey Papers. Mines and Geology Branch, Canada* 64 (11): 1-100.
- KAKABADZE, M. V. 1978. On the systematic and stratigraphical significance of the genera *Pseudocriocerat* Spath, *Adoulicerat* Thomel and *Kutatissites* Kakabadze. *Annales du Musée d'histoire naturelle de Nice* 1976 (4): XXXIV.1-XXXIV.5.
- KAKABADZE, M. V. 1981. [The ancyloceratids of the south of the USSR and their stratigraphic significance]. *Trudy Geologicheskogo instituta. Akademiya nauk Gruzinskoi SSR* (n.s.) 71: 1-196. (In Russian.)
- KEMPER, E., RAWSON, P. F. & THIEULOY, J. P. 1981. Ammonites of Tethyan ancestry in the early Lower Cretaceous of north-west Europe. *Palaeontology* 24 (2): 251-311.
- KENNEDY, W. J. & KLINGER, H. C. 1975. Cretaceous faunas from Zululand and Natal, South Africa. Introduction, Stratigraphy. *Bulletin of the British Museum (Natural History)* (Geology) 25 (4): 263-315.
- KENNEDY, W. J. & KLINGER, H. C. 1979. Cretaceous faunas from Zululand and Natal, South Africa. The ammonite superfamily Haplocerataceae Zittel, 1884. *Annals of the South African Museum* 77 (6): 85-121.
- KENNEDY, W. J. & KLINGER, H. C. 1990. Cretaceous faunas from Zululand and Natal, South Africa. *Hatchericeras* Stanton, 1901 (Cephalopoda, Ammonoidea), from the Barremian of Zululand. *Annals of the South African Museum* 99 (8): 231-243.
- KILIAN, W. 1895. Notice stratigraphique sur les environs de Sisteron et contribution à la connaissance des terrains secondaires du Sud-Est de la France. *Bulletin de la Société géologique de France* (3e sér) 23: 659-803.
- KLINGER, H. C. 1976. Cretaceous heteromorph ammonites from Zululand. *Memoirs. Geological Survey. Republic of South Africa* 69: 1-142.

- KLINGER, H. C. 1990. Upper Barremian Heteroceratinae (Ammonoidea) from Caucasus, Zululand and Patagonia: palaeobiogeographic significance. *Cretaceous Research* **11** (3): 321–329.
- KLINGER, H. C., KAKABADZE, M. V. & KENNEDY, W. J. 1984. Upper Barremian (Cretaceous) heteroceratid ammonites from South Africa and the Caucasus and their palaeobiogeographic significance. *Journal of Molluscan Studies* **50** (1): 43–60.
- KLINGER, H. C. & KENNEDY, W. J. 1977. Cretaceous faunas from Zululand, South Africa, and southern Mozambique. The Aptian Ancyloceratidae (Ammonoidea). *Annals of the South African Museum* **73** (9): 215–359.
- KOENEN, A. VON. 1902. Die Ammonitiden des Norddeutschen Neocom (Valanginien; Haute-rivien; Barrémien und Aptien). *Abhandlungen der Königlich preussischen geologischen Landesanstalt und Bergakademie* (n.f.) **24**: 1–451. Berlin.
- KOTETISHVILI, E. V. 1970. Stratigrafia i fauna kolchiditogo i smeshnix gorizontov zapadnoi gruzi. *Trudy Geologicheskogo instituta. Akademiya nauk Gruzinskoi SSR* (n.s.) **25**: 5–116.
- KULLMANN, J. & WIEDMANN, J. 1970. Significance of sutures in phylogeny of Ammonoidea. *Paleontological Contributions. University Kansas* **47**: 1–32.
- LAPEYRE, J. F. 1974. Révision de l'ammonite-index *Pseudothurmannia angulicostata* d'Orbigny. *Annales du Musée d'Histoire naturelle de Nice* **2**: 81–87.
- LEANZA, A. F. 1970. Ammonites nuevos o poco conocidos del Aptiano, Albiano y Cenomaniano de los Andes Australes con notas acerca de su posición estratigráfica. *Revista de la Asociación geológica argentina* **25** (2): 197–261.
- LEVEILLÉ, C. 1837. Description de quelques nouvelles coquilles fossiles du département des Basses-Alpes. *Mémoires de la Société géologique de France* **2**: 313–315.
- MANOLOV, J. R. 1962. New ammonites from the Barremian of North Bulgaria. *Palaentology* **5** (3): 527–539.
- MEEK, F. B. 1876. A report of the invertebrate Cretaceous and Tertiary fossils of the Upper Missouri country. In: HAYDEN, F. V. *Report of the United States Geological Survey of the Territories* **9**: lxiv, 1–629.
- MÜLLER, G. 1892. Über das Vorkommen von *Ancyloceras gigas*-Schichten bei Mellendorf nördlich von Hannover. *Jahrbuch der Königlich preussischen geologischen Landesanstalt* **13**: 16–22.
- MURPHY, M. A. 1975. Paleontology and stratigraphy of the Lower Chickabally Mudstone (Barremian–Aptian) in the Ono Quadrangle, Northern California. *University of California Publications in Geological Sciences* **113**: 1–52.
- MYCZYNSKI, R. 1977. Lower Cretaceous ammonites from Sierra del Rosario (Western Cuba). *Acta paleontologica polonica* **22** (2): 139–173.
- NEUMAYR, M. & UHLIG, V. 1881. Ueber Ammonitiden aus den Hilfsbildungen Deutschlands. *Palaentographica* **27**: 129–203.
- NOLAN, H. 1894. Sur les *Crioceras* du groupe du *Crioceras Duvali*. *Bulletin de la Société géologique de France* (3e sér) **22**: 183–196.
- OBATA, I., HAWIGARA, S. & KAMIKO, S. 1975. Geological age of the Cretaceous Chosi Group. *Bulletin of the National Science Museum* (Series C, Geology and Paleontology) **1** (1): 17–36. [In Japanese.]
- OBATA, I. & MATSUKAWA, M. 1984. A Barremian occurrence of an olcostephanid, a perisphinctacean ammonite, from the Chosi Group, Japan. *Bulletin of the National Science Museum* (Series C, Geology & Paleontology) **10** (4): 169–180.
- OBATA, I., MATSUKAWA, M., TSUDA, H., FUTAKAMI, M. & OGAWA, Y. 1976. Geological age of the Cretaceous Ishido Formation, Japan. *Bulletin of the National Science Museum* (Series C, Geology & Paleontology) **2** (3): 21–138.
- OBATA, I., MAYIA, S., INOUE, Y. & MATSUKAWA, M. 1982. Integrated mega- and micro-fossil biostratigraphy of the Lower Cretaceous Chosi Group, Japan. *Bulletin of the National Science Museum* (Series C, Geology & Paleontology) **8** (4): 145–179.
- OBATA, I. & OGAWA, Y. 1976. Ammonite biostratigraphy of the Cretaceous Arida Formation, Wakayama Prefecture. *Bulletin of the National Science Museum* (Series C, Geology & Paleontology) **2** (2): 93–110.
- OOSTER, W. A. 1860. Catalogue des Céphalopodes fossiles des Alpes suisses, 5 ème partie. *Nouveaux mémoires de la Société helvétique des sciences naturelles* **18**: 1–100.

- ORBIGNY, A. D' 1840-1842. *Paléontologie française: Terrains crétacés. 1. Céphalopodes*: 1-120 (1840); 121-430 (1841); 431-662 (1842). Paris: Masson.
- ORBIGNY, A. D' 1850. *Prodrome de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés* 2: 1-428. Paris: Masson.
- PARONA, C. F. 1898. Descrizione di alcune Ammoniti del Neocomiano veneto. *Palaeontographia italica* 3: 137-144.
- PHILLIPS, J. 1829. *Illustrations of the geology of Yorkshire; or, a description of the strata and organic remains of the Yorkshire Coast*. York.
- PICTET, J. F. & LORIOL, P. DE 1858-59. Description des fossiles contenus dans le terrain néocomien des Voirons. *Mat. Paléontologique Suisse* (2): 1-64.
- RAWSON, P. F. 1975. The interpretation of the Lower Cretaceous heteromorph ammonite genera *Paracrioceras* and *Hoplocrioceras* Spath, 1924. *Palaeontology* 18 (2): 275-283.
- RAWSON, P. F. 1983. The Valanginian to Aptian stages—current definitions and outstanding problems. *Zitteliana* 10: 493-500.
- RAWSON, P. F. & MUTTERLOSE, J. 1983. Stratigraphy of the Lower B and basal Cement Beds (Barremian) of the Speeton Clay, Yorkshire, England. *Proceedings of the Geologists' Association* 94 (2): 133-146.
- RENNGARTEN, V. 1926. La faune des dépôts crétacés de la région d'Assakambileevka, Caucase du Nord. *Trudy Geologicheskogo komiteta. St. Petersburg* 147: 1-132.
- RICCARDI, A. C. 1984a. Las Asociaciones de Amonitas del Jurásico y Cretácico de la Argentina. *Actas. Noveno Congreso Geológico Argentino* 4: 559-595.
- RICCARDI, A. C. 1984b. Las Zonas de Amonitas del Cretácico de la Patagonia (Argentina y Chile). *Memoria. III Congreso Latinoamericano de Paleontología, México, 1984*: 396-405.
- RICCARDI, A. C. 1988. The Cretaceous system of southern South America. *Memoirs. Geological Society of America* 168: 1-161.
- RICCARDI, A. C. & AGUIRRE URRETA, M. B. 1989. Hemihoplittid ammonoids from the Lower Cretaceous of Southern Patagonia. *Palaeontology* 32 (2): 447-462.
- RICCARDI, A. C., AGUIRRE URRETA, M. B. & MEDINA, F. A. 1987. Aconeceratidae (Ammonitina) from the Hauterivian-Albian of Southern Patagonia. *Palaeontographica* (A) 196 (4-6): 105-185.
- ROCH, E. 1930. Etudes géologiques dans la région méridionale du Maroc occidental. Thèse, Paris.
- ROEMER, F. A. 1841. *Die Versteinerungen des norddeutschen Kreidegebirges*. Hannover.
- ROMAN, F. 1938. *Les ammonites Jurassiques et Crétacées*. Paris: Masson.
- ROUCHADZE, J. 1933. Les ammonites aptiennes de la Géorgie occidentale. *Bulletin de l'Institut géologique de Géorgie* 1: 165-273.
- ROUCHADZE, J. 1938. Céphalopodes nouveaux ou peu connus de l'Aptien de la Géorgie. *Bulletin de l'Institut géologique de Géorgie* 3: 129-189.
- ROYO Y GÓMEZ, J. 1945. Fósiles del Barremiense Colombiano. *Compilación de los estudios geológicos oficiales en Colombia* 6: 459-494.
- SARASIN, C. & SCHÖNDELMAYER, C. 1901-2. Etude monographique des Ammonites du Crétacé inférieur de Châtel au Saint-Denis. *Mémoire de la Société paléontologique suisse* 28-29: 1-195.
- SARKAR, S. S. 1954. Some new genera of uncoiled ammonites from Lower Cretaceous. *Science and Culture* 19: 618-620.
- SARKAR, S. S. 1955. Révision des Ammonites déroulées du Crétacé inférieur du Sud-Est de la France. *Mémoires de la Société géologique de France* (n.s.) 34: 1-176.
- SARKAR, S. S. 1977. Sur *Binellicer* genre nouveau d'Heteromorpha et sur la validité du genre *Emericeras* Sarkar, 1954. *Paläontologische Zeitschrift* 51 (3-4): 258-261.
- SIMIONESCU, I. M. 1900. Note sur quelques ammonites du néocomien français. *Travaux du Laboratoire géologie de la Faculté des sciences de l'Université Grenoble* 5: 1-17.
- SKWARKO, S. K. & THIEULOUY, J. P. 1989. Early Barremian (Early Cretaceous) mollusca from western Irian Jaya, Indonesia. *Publication of the Geological Research and Development Centre, Republic of Indonesia* (Palaeontology) 6: 26-42.
- SORNAY, J. 1968. Sur des ammonites du Barrémien et de l'Aptien d'Ibiza (Baléares). *Annales scientifiques de l'Université de Besançon (Géologie)* 5: 3-8.

- SPATH, L. F. 1924. On the ammonites of the Speeton Clay and the subdivisions of the Neocomian. *Geological Magazine* 61: 73–89.
- SPATH, L. F. 1930. On the Cephalopoda of the Uitenhage Beds. *Annals of the South African Museum* 28 (2): 131–157.
- STANTON, T. W. 1901. The marine Cretaceous invertebrates. *Report of the Princeton University Expeditions to Patagonia* 1: 1–43.
- TAVANI, G. 1942. Paleontologia della Somalia. III. Fossili del Cretaceo. Molluschi del Cretaceo della Somalia. *Palaeontographia italica* 32 (supl. 4): 7–47 (93–133).
- THIEULOY, J. P. 1964. Un Céphalopode remarquable de l'Hauteriviens basal de la Drôme: *Himantoceras* nov. gen. *Bulletin de la Société géologique de France* (6) 7: 205–213.
- THIEULOY, J. P. 1966. Leptocères berriasiens du massif de la Grande-Chartreuse. *Travaux du Laboratoire de géologie de la Faculté des sciences de l'Université de Grenoble* 42: 281–295.
- THIEULOY, J. P. 1979. *Matheronites limentinus* n. sp. (Ammonoidea). Espèce-type d'un horizon-répère Barrémien Supérieur du Vercors Méridional (Massif Subalpin Français). *Géobios, Mémoire spécial* 3: 305–317.
- THIEULOY, J. P. & THOMEL, G. 1964. Sur l'utilisation éventuelle des Ammonites déroulées dans la chronologie du Crétacé inférieur. *Travaux du Laboratoire de géologie de la Faculté des sciences de l'Université de Grenoble* 40: 121–126.
- THOMEL, G. 1964. Contribution à la connaissance des céphalopodes Crétacés du sud-est de la France. Note sur les ammonites déroulées du crétacé inférieur. *Mémoires de la Société géologique de France* (n.s.) 43 (2): 1–80.
- THOMEL, G. 1965. Contribution à la connaissance des céphalopodes Crétacés du sud-est de la France. Sur deux espèces du Crétacé inférieur des Basses-Alpes. *Bulletin de la Société géologique de France* (7) 7: 417–420.
- THOMEL, G. 1981. *Ammonites*. Saint-Laurent-du-Var: Editions Serre.
- THOMEL, G., DELANOY, G., COULLET, P., DAVOUX, J., FUHR, F., FUHR, M., GAZEL, L., GIVERSO, J., JULLIAN, H., JULLIAN, V., LEVAN, G., MASCARELLI, E., MAUREL, L., POUPON, A. & SALOMON, M. 1990. Le genre *Acrioceras* Hyatt, 1900 dans le Barrémien du sud-est de la France. *Annales du Musée d'histoire naturelle de Nice* 7: 20–110.
- THOMEL, G., DELANOY, G. & AUTRAN, G. 1987. Valeur taxonomique, position stratigraphique et relations phylétiques des genres d'Ammonoidea: *Acrioceras* Hyatt, 1900 et *Aspinoceras* Anderson, 1938 au cours des temps hauteriviens, ainsi que de leurs dérivés. *Compte rendu de l'Académie des sciences, Paris* (2) 305: 215–219.
- THOMSON, M. R. A. 1971. Ammonite faunas of south-eastern Alexander Island and their stratigraphical significance. In: ADIE, R. J. ed. *Antarctic geology and geophysics*: 155–160. Oslo: Universitetsforlaget.
- THOMSON, M. R. A. 1974. Ammonite faunas of the Lower Cretaceous of South-eastern Alexander Island. *Scientific Reports. British Antarctic Survey* 80: 1–44.
- THOMSON, M. R. A. 1980. Mesozoic ammonite faunas of Antarctica and the break-up of Gondwana. *Fifth International Gondwana Symposium, Wellington, New Zealand, 11–16 February 1980*: 269–275.
- THOMSON, M. R. A. 1983. 'European' ammonites in the Lower Cretaceous of Antarctica. *Zitteliana* 10: 407–412.
- TORCAPEL, A. 1884. Quelques fossiles nouveaux de l'Urgonien du Languedoc. *Bulletin de la Société des sciences naturelles, Nîmes* 9–11: 1–12.
- UHLIG, V. 1883. Die Cephalopoden der Wernsdorfer-Schichten. *Denkschrift der K. Akademie der Wissenschaften. Wien. (Mathematisch-Naturwissenschaften Klasse)* 46: 127–290.
- VÁŠIČEK, Z. & MICHALÍK, J. 1988. Some heteromorphic ammonites from Polomec (Hauterivian-Barremian, Central Western Carpathians, Czechoslovakia). *Geologický sborník* 39 (6): 655–674.
- WEAVER, C. 1931. Paleontology of the Jurassic and Cretaceous of West Central Argentina. *Memoirs of the University of Washington* 1: 1–469.
- WEDEKIND, R. 1916. Über Lobus, Suturallobus und Inzision. *Zentralblatt für Mineralogie, Geologie und Paläontologie* (B) 8: 185–195.
- WIEDMANN, J. 1962. Unterkreide-Ammoniten von Mallorca. 1. Lieferung: Lytoceratina, Aptychi. *Abhandlungen der Mathematisch-naturwissenschaftliche Klasse. Akademie der Wissenschaften und der Literatur* 1962 (1): 1–148.

- WIEDMANN, J. 1966. Stammesgeschichte und System der Posttriadischen Ammonoideen. *Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen* 127: 13-81.
- WIEDMANN, J. 1973. Ancyloceratina (Ammonoidea) at the Jurassic/Cretaceous Boundary. In: HALLAM, A. ed. *Atlas of paleobiogeography*: 309-316. Amsterdam, London, New York: Elsevier.
- WRIGHT, C. W. 1952. A classification of the Cretaceous ammonites. *Journal of Paleontology* 26 (2): 213-222.
- WRIGHT, C. W. 1957. Cephalopoda Ammonoidea. In: MOORE, R. C. ed. *Treatise on Invertebrate Paleontology. Part L, Mollusca* 4: xxii, L1-L490. New York: Geological Society of America; Lawrence, Kansas: University of Kansas Press.
- WRIGHT, C. W. 1981. Cretaceous Ammonoidea.: In: HOUSE, M. R. & SENIOR, J. R. eds. *The Ammonoidea. Systematics Association. Special Volume* 18: 157-174.
- YENNE, K. 1949. *Pedioceras*, a synonym of *Crioceras* (*Pseudocrioceras*). *Journal of Paleontology* 23: 623-624.

